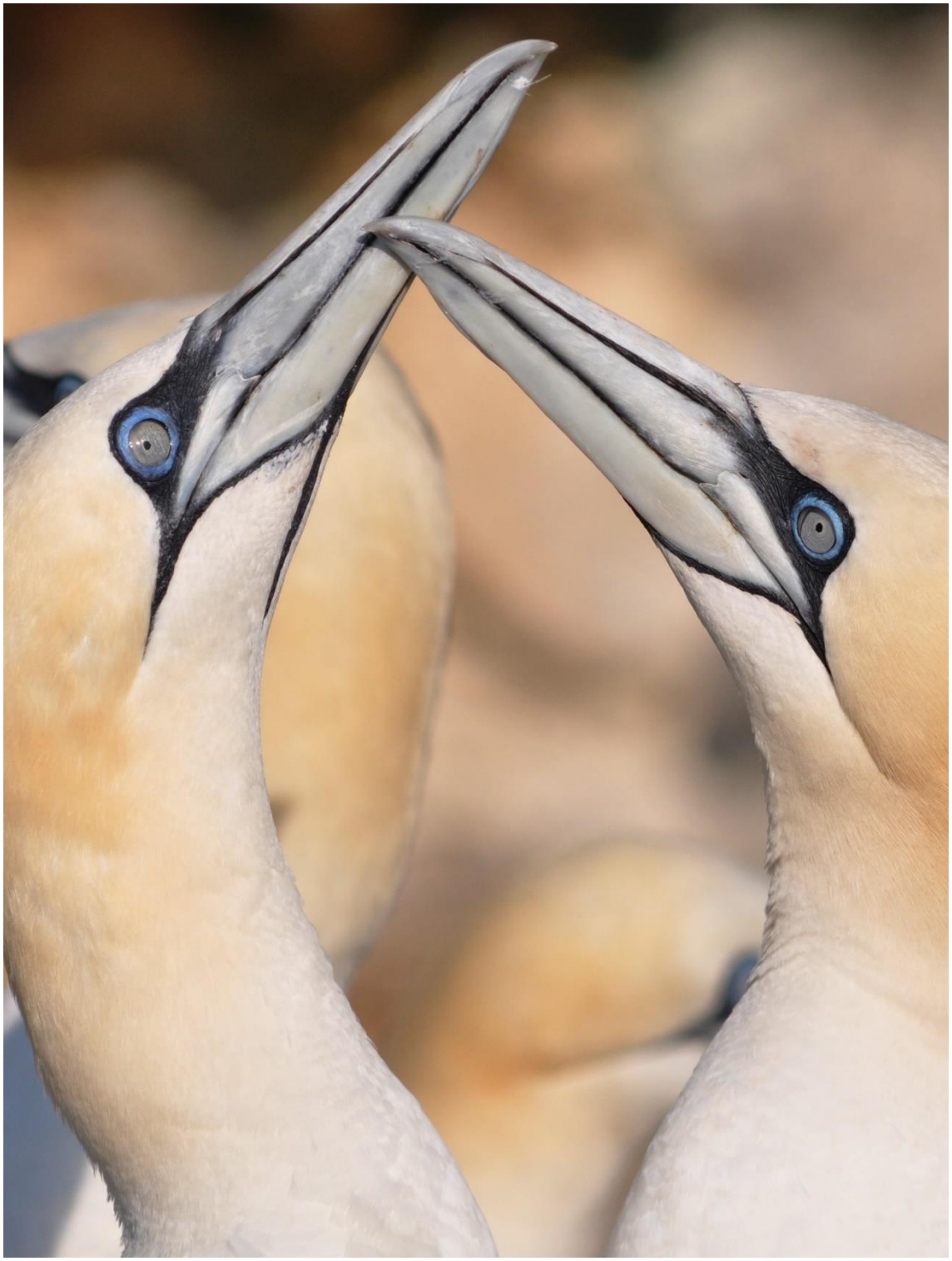
Northern gannet *Morus bassanus* foraging ecology:
A multidimensional approach

Submitted by Bethany Louise Clark, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences in July 2019.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

Signature……



Thesis abstract

This thesis brings together multiple strands of information at different temporal and spatial scales to shed new light on foraging behaviour. Foraging accounts for much of the time and energy budgets of wild animals and underpins many ecological and evolutionary processes. I used the central place foraging trips of a wide-ranging marine predator, the northern gannet *Morus bassanus,* as a model to study foraging ecology and the influences of fisheries and climate change. My five data chapters span a range of temporal scales, from two-second behavioural classification to interannual variation across 11 years, as well as a range of spatial scales from individual bird-boat interactions to a multi-colony comparison spanning 83% of the latitudinal range of breeding colonies. First, I found sex-specific foraging behaviour across a range of spatial, temporal and isotopic axes and that the extent of segregation varied inter-annually. Second, I examined the energetics of foraging behaviour, revealing the relative costs of different behaviours and how they relate to three-dimensional flight patterns. I found that effort was driven by the time spent performing behaviours rather than differences in the costs of behaviours per unit time. Furthermore, the proportions of each trip spent performing each behaviour were independent of trip length, meaning that foraging trip duration was a good metric of overall effort. Third, I used bird-borne videos cameras to reveal a high incidence of gannets scavenging from fisheries discards and trawl nets in the Celtic Sea. Scavenging is often thought to be an energy-saving strategy, but the energetic cost of scavenging was no different from that of natural foraging. Fourth, I found that gannets did not respond to nearby fishing vessels in Iceland, where discarding is banned and foraging effort suggested plentiful natural prey. Finally, I collated a large multi-colony dataset, which showed that foraging range and trip durations decreased with latitude when controlling for colony size. I related this pattern to poleward range shifting in response to climate change. Overall, I found that foraging behaviour is highly variable in some respects and consistent in others. This is driven by stable factors such as sex and colony location and changing factors such as population size, climate and oceanography, and fisheries practice or policy. This thesis particularly highlights the benefits of combining data from multiple sources, time periods and regions in order to reveal new patterns.

Acknowledgements

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I also thank Richard Phillips and Brendan Godley for examining my thesis and providing constructive comments.

“It doesn’t matter! It is in the past!” “Yeah, but it still hurts.” “Ah yes, the past can hurt. But the way I see it, you can either run from it, or learn from it.”

– Rafiki, The Lion King, 1994.

In some ways, my PhD experience was shaped by a single moment resulting in a small but complex wrist fracture. I have a friend who always answers numerical questions with uncertain answers with “about five”. After five data chapters, five years and five surgeries, it turns out that she was right all along. As such, I need to thank everyone else who has helped me to this point:

Steve for guiding me through the many twists and turns of my PhD, and for putting up with me for much longer than intended.

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And of course, the gannets for putting up with me bothering them over the years. The following quotes from The Gannet, J. H. Gurney, 1913, illustrate how I have come to admire their spirit:

"When it gets hold with its beak of a man's clothes or any other object, it holds fast and never lets go before it is dead, which makes the catch easier; but the man must take care of himself, that the birds should not get hold of his hands, for that would hinder him in his work."

– H. C. Müller, 1869.

And also, their amazing behaviours:

"Raising himself high into the air he precipitates himself under water like an arrow." – F. Faber, 1822.

But not their flavour:

"… the flesh is eaten, for it is bravely fat and rich, but on that account oily." – E. Olafsen & B Povelsen, 1772.

"…therefore not so palatable to foreigners…" – N Mohr, 1786.

"The lemon is in play." – in Qikiqtajuaq, J. Finnemore, 2011.

Contents

Author's Declaration

All work in this thesis was completed by BL Clark with the contributions from co-authors outlined below.

Chapter 2 - SL Cox, KM Atkins, S Bearhop, AWJ Bicknell, TW Bodey, IR Cleasby, WJ Grecian, KC Hamer, BR Loveday, PI Miller, G Morgan, L Morgan, J Newton, SC Patrick, KL Scales, RB Sherley, F Vigfúsdóttir, ED Wakefield, MJ Witt & SC Votier

BLC, SCV and KMA designed the study. BLC, SLC, RBS, FV, KMA, LM, GM, SCP, TWB, AWJB, EDW, KCH, SB, WJG, KLS and SCV collected the field data. PIM, BRL and MJW accessed and processed the habitat data. BLC, FV and JN conducted laboratory work. BLC, SLC, RBS and IRC planned and performed the analysis. SCV, SLC, IRC, RBS and FV commented on the text.

Chapter 3 - JPY Arnould, MR Wells, IR Cleasby, ED Wakefield, J Rudd, LA Hawkes & SC Votier

BLC and SCV designed the study. BLC, JPYA, MRW and SCV collected the data. BLC and ED coded the videos. BLC, IRC, EDW and JR processed the data. BLC performed the analysis. SCV and LAH commented on the text.

Chapter 4 - JPY Arnould, MR Wells, LA Hawkes, L Morgan, G Morgan, E Dwan & SC Votier

BLC and SCV designed the study. BLC, JPYA, MRW, LM, GM, ED and SCV collected the data. BLC, ED and JR processed the data. BLC performed the analysis. SCV and LAH commented on the text.

Chapter 5 - F Vigfúsdóttir, MJ Jessopp, JM Burgos, TW Bodey & SC Votier

BLC, SCV and FV designed the study. BLC and FV collected the bird tracking and diet data. JMB accessed and processed the vessel location data. BLC, MJJ and TWB planned and performed the analysis. All commented on the text.

Chapter 6 - F Vigfúsdóttir, TW Bodey, S Wanless, KC Hamer, J Blackburn, WA Montevecchi, S Garthe, ED Wakefield, SL Cox & SC Votier

BLC designed the study. BLC, FV, TWB, SW, KCH, JB, WAM, SG, EDW, SLC and SV collected the field data. BLC and SLC processed the data. SCV, SW, KH, FV and TWB commented on the text.

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Chapter 1 – General Introduction

1.1 A multidimensional view of ecology

While many ecological questions can be answered by measuring one or two axes of variation, bringing many together can provide new insights. Niche segregation occurs along many axes, including space, time, habitat, diet and parental roles (Hutchinson, 1961; Levine & Hillerislambers, 2009; Selander, 1966). However, few niche partitioning studies measure multiple dimensions simultaneously. MacArthur's warblers provide a key example (MacArthur, 1958), where several warbler species were thought to occupy the same space and, therefore, ecological niche, apparently conflicting with niche theory. However, MacArthur showed that the warblers segregated vertically despite their spatial overlap from a two-dimensional perspective. Moreover, niche space can vary in response to changing environmental conditions, such as food availability (Ishikawa & Watanuki, 2002). We have a growing ability to investigate this topic as new technology allows us to observe wild animals across more spatial dimensions, at finer resolutions, over longer time periods and with more channels of information for context (Holyoak *et al.,* 2008). Bio-logging, the attachment of recording or transmitting devices to animals, has provided a host of techniques for studying previously unobserved behaviours, life stages, locations and habitats (Ropert-coudert & Wilson, 2005). Recent improvements in sensor type, cost, size, memory, resolution, durability and attachment design have facilitated huge leaps forward in understanding animal space-use, particularly for birds and marine animals that are difficult to observe directly (Hussey *et al.,* 2015; Kays *et al.,* 2015).

Bio-logging has transformed the study of animal movement, but studies have largely recorded movement in only one or two spatial dimensions. Investigations of height or depth are often independent of the analysis of movement in two dimensions (Belant *et al.,* 2012). A key goal is to reconstruct three-dimensional movement, as many animals use space in a truly three-dimensional way, by swimming, climbing or flying through habitats that are aquatic, aerial or vertically structured (Bailleul *et al.,* 2010). For example, measuring altitude can shed light on the energy use of flying animals. Loss of altitude during flight can represent potential energy lost, but soaring does not require significant energetic effort when animals exploit rising air such as updrafts and thermals (De Monte *et al.,* 2012; Shepard *et al.,* 2011). A similar situation can occur with diving species that must expend energy to overcome their

buoyancy at the surface to reach the depths at which their food lives (Nowacek *et al.,* 2001). Practical applications for measuring movement in three dimensions include using the flight height of birds and bats in collision risk models to inform the optimal positioning of wind turbines to reduce collisions both at sea (Corman & Garthe, 2014; Shannon *et al.,* 2014) and over land (Johnston *et al.,* 2013; Katzner *et al.,* 2012). Additionally, discovering the flight heights of migrating birds in relation to aircraft flyways could reduce the incidence of bird strike that can be a substantial threat to aircraft safety (DeVault *et al.,* 2005).

On a finer scale, tri-axial accelerometers measure exactly how animals move across the axes of surge, heave and sway (Figure 1.1). Accelerometry can be used to identify behaviours (Shepard *et al.,* 2008) and the energetic costs of activities (Halsey *et al.,* 2009; Wilson *et al.,* 2006). By combining geolocators and accelerometers, Liechti *et al.* (2013) provided the first clear evidence that Alpine swifts *Tachymarptis melba* fly continuously for 200 days, even sleeping on the wing. Improving data resolution allows new questions to be asked – recording GPS at 5hz and acceleration at 300hz made it possible to detect the subtle aerodynamic benefits of avian 'V' formations (Portugal *et al.,* 2014).

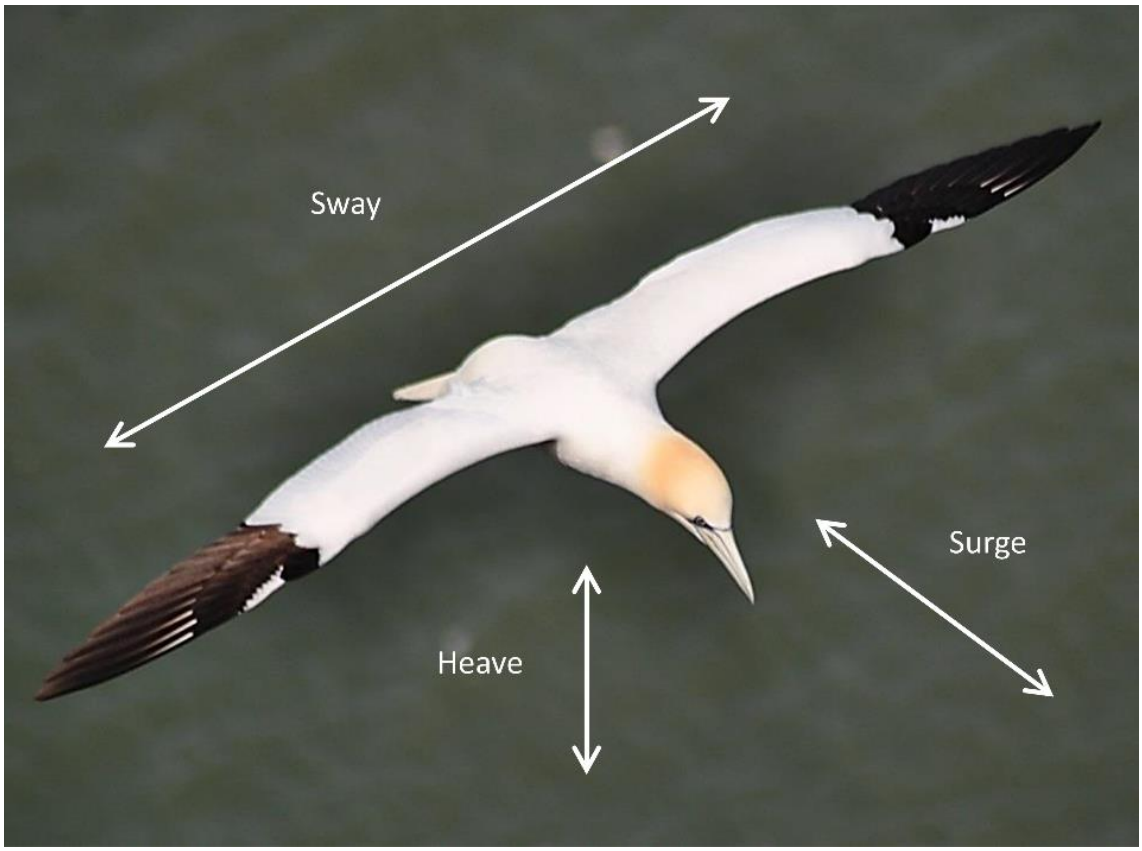


Figure 1.1. Movement recorded by accelerometers in the surge, heave and sway axes.

Linking movement with other channels of information can provide further insights. For example, combined video cameras, accelerometers and temperature-depth recorders revealed that ocean sunfish *Mola mola* dive to 100-200m depth to forage on siphonophores, then return to the surface to increase their body temperature (Nakamura *et al.,* 2015). Animal-borne loggers can also be used to observe the environment. For example, king penguins *Aptenodytes patagonicus*, fitted with temperature and dive depth loggers have been used to map the thermal profile of the underwater environment at unprecedented resolution offshore from the remote Kerguelen Islands, shedding new light on the oceanography of this region (Charrassin *et al.,* 2002).

Novel combinations of existing methods, and large temporal or spatial scales, allow bio-logging studies to answer broader ecological questions as well as describing unknown behaviours or distributions. Studies are further enhanced by relating bio-logging data with other information, such as population size, diet, biometrics, genetics, breeding success and habitat information.

1.2 Foraging behaviour

Foraging behaviour is crucial to the lives of almost all wild animals (Stephens & Krebs, 1986), and often accounts for the majority of their time and energy budgets. Animals should aim to maximise foraging efficiency (Emlen, 1966; Macarthur & Pianka, 1966), particularly when feeding offspring (Kacelnik, 1984). As such, foraging underpins much of ecology and behaviour, shaping distributions, community structures and evolutionary trajectories (Kondoh, 2003; McNab, 1963; Stephens & Krebs, 1986).

The study of foraging benefits greatly from a multidimensional perspective as foraging behaviours, including commuting, searching and prey capture, cannot always be directly observed (Kays *et al.,* 2015). It is possible to directly detect prey capture events using specific bio-loggers such as animal-borne cameras (Watanabe & Takahashi, 2013), head-mounted accelerometers (Kokubun *et al.,* 2011), and stomach (Garthe *et al.,* 1999) or oesophageal temperature sensors (Charrassin *et al.,* 2001). However, most studies instead rely on behavioural proxies for prey capture such as diving or searching behaviours. When food is unpredictable and patchily distributed, searching behaviour is generally characterised by slow or tortuous movement, in contrast to fast, straight commuting (Andersson, 1981; Fauchald & Tveraa, 2003). Analytical methods

that categorise area-restricted search from GPS tracks include first-passage time (Pinaud, 2008), state-space models (Jonsen *et al.,* 2013), hidden Markov models (Michelot *et al.,* 2016) and speed/tortuosity thresholds (Wakefield *et al.,* 2013). By combining these data with information about the underlying habitats, we can understand the processes by which animals find food.

1.3 Seabirds as a model

Breeding seabirds provide a good model for the study of foraging behaviour because they nest on land but forage at sea. This provides clear boundaries between the habitat required for breeding and that for feeding, and this constraint is a driver of the evolutionary characteristics of seabirds (Coulson, 2002). Suitable breeding sites that are inaccessible to terrestrial predators are rare (Rolland *et al.,* 1998), and so foraging habitats are often distant from breeding colonies. Consequently, the effort required to reach foraging sites is an important aspect of seabird time and energy budgets. The energetic costs of foraging are crucial for seabirds because chicks develop slowly, so, generally, both parents have to provision them for an extended period. Colonial lifestyles increase these costs as the density of conspecifics surrounding the colony forces individuals to forage even further afield to avoid competition (Ashmole, 1963; Lewis *et al.,* 2001), particularly when other colonies are nearby (Corman *et al.,* 2016; Wakefield *et al.,* 2013).

Many seabirds are suitable for multi-channel bio-logging studies as they are large and robust, and return to the nest for extended periods, thus allowing safe deployment and a high probability of recapturing archival tags. Most seabirds travel above the water's surface where GPS satellites are available, making them well-suited to bio-logging compared to many marine species. Their social monogamy helps us to investigate sex-differences in foraging behaviour during times when both males and females are constrained to similar foraging areas (Lack, 1968). Marine birds are also indicators for ocean health (Parsons *et al.,* 2008), reflecting the impacts of changes in fish populations (Robinette *et al.,* 2007) and climate (Springer *et al.,* 2007). Furthermore, as seabirds tend to breed in restricted sites that are well-monitored, seabird foraging behaviour can be easily linked to population counts and processes. Finally, seabirds are generally conspicuous and easy to count, and so there is a long history of studying seabirds at breeding colonies (Gurney, 1913).

Human activities alter seabird foraging habitats, presenting both threats and opportunities. Commercial fishing can be a major threat by depleting prey stocks (Pauly *et al.,* 1998), damaging benthic habitats (Kaiser & Spencer, 1996; Shester & Micheli, 2011) and causing incidental mortality (Lewison *et al.,* 2012). However, fisheries also discard approximately 10 million tonnes of bycatch per year (Zeller *et al.,* 2018), which supplements the diets of many seabirds (Bicknell *et al.,* 2013; Furness, 2003; Garthe *et al.,* 1996). This subsidy is so abundant that it may have artificially inflated populations of some species, potentially making them vulnerable if discards become unavailable because of changes in fish stocks or fishing policy (Fondo *et al.,* 2015; Oro *et al.,* 1995). As marine fish populations are unsustainably exploited around the globe (Halpern *et al.,* 2008; Pauly *et al.,* 1998), discard bans are planned or implemented in many regions (Commission of European Communities, 2009; Popsescu & Poulsen, 2012). Understanding the relationship between seabirds and fishery discards is vital for incorporating effective conservation measures into fisheries policy and marine spatial planning (Bicknell *et al.,* 2013). Additionally, climate change affects marine systems at a global scale (Parmesan & Yohe, 2003), which is thought to mainly impact seabirds by altering prey abundance and distribution (Bertram *et al.,* 2009; Sydeman *et al.,* 2012; Thackeray *et al.,* 2010). Many species shift their distributions poleward to track favourable conditions (Chen *et al.,* 2012; Hickling *et al.,* 2006), including many seabird prey species (Atkinson *et al.,* 2019; Perry *et al.,* 2005). However, seabirds are site faithful (Bried & Jouventin, 2002) with limited potential breeding sites, and we know little about how colonial species may be able to respond to environmental change (Matthiopoulos *et al.,* 2005), particularly in terms of colony formation (Coulson, 2002).

1.4 Study species: the northern gannet

The northern gannet *Morus bassanus* (hereafter “gannet”) is the largest of the Sulidae, a family of plunge-diving seabirds. Gannets are highly colonial with a North Atlantic breeding range in both western Europe and eastern Canada (Figure 1.2, Murray *et al.,* 2015a). Gannets are faithful to their breeding site and return each year for a long breeding season, consisting of an incubation period of ~44 days and a chick-rearing period of ~90 days (Nelson, 2002).

Gannets provide a useful model for studying seabird foraging behaviour due to their history of study and amenability for bio-logging. The gannet has a rich tradition of observation due to its conspicuous nature both at sea and at breeding colonies (Nelson, 2002). In fact, the gannet was the first bird species for which anyone attempted to estimate the global population with 50,500 breeding pairs estimated in 1910 (Gurney, 1913). This inspired a more robust count between 1914 and 1935 (Wynne Edwards *et al.,* 1936), and the population status is now well known across its range (Barrett *et al.,* 2017; Chardine *et al.,* 2013; Garðarsson, 2019; Murray *et al.,* 2015a). Populations are increasing, with now 10-fold as many breeding gannets as were recorded 100 years ago (Table 1.1). This population growth followed an estimated decline (Fisher & Vevers, 1944), associated with harvesting for meat, feathers and oil (Montevecchi & Hufthammer, 1990; Serjeantson, 2001). Consequently, we can investigate the processes affecting poleward range expansion as the gannet recolonises Norway (Barrett *et al.,* 2017), where recorded skeletal remains date from approximately 800 to 7000 years ago (Montevecchi & Hufthammer, 1990). However, gannets are still exposed to many anthropogenic threats (Croxall *et al.,* 2012), including wind turbine collision (Cleasby *et al.,* 2015a), bycatch (Oliveira *et al.,* 2015; Žydelis *et al.,* 2013), entanglement with plastic at the nest (Votier *et al.,* 2011), oil spills (Montevecchi *et al.,* 2012a), and climate change (Montevecchi *et al.,* 2013). Furthermore, the closely related Cape gannet *Morus capensis* was recently classified as endangered (BirdLife International, 2018), and so, insights into northern gannet ecology may also be useful for protecting Cape gannets and other similar species.

As the largest sulid worldwide, and the largest seabird in the North Atlantic, gannets provide a suitable species for testing new loggers and logger combinations (Vandenabeele *et al.,* 2014). As such, we have information across a wide range of dimensions from archival and transmitting GPS loggers, dive depth recorders, altitude loggers, accelerometers and video cameras (Cleasby *et al., 2015a*; Cox *et al.,* 2016; Ropert-Coudert *et al.,* 2009; Votier *et al.,* 2013). Furthermore, due to the large size of the gannet, more affordable, heavier loggers can be used, increasing the numbers of tagged individuals. As such, gannets have been satellite tracked at many colonies across their range and at some colonies over many years (Pettex *et al.,* 2012; Wakefield *et al.,* 2013). The unique spatial and temporal coverage of tracking data makes it possible to investigate

both interannual variation and large-scale environmental gradients in behaviour. We can also bring in remotely sensed data such as oceanography or fishing vessel locations to assess the drivers of foraging decisions (Bodey *et al.,* 2014; Cox *et al.,* 2016), methods that are becoming more accessible to those other than analytical specialists (Clark *et al.,* 2016).

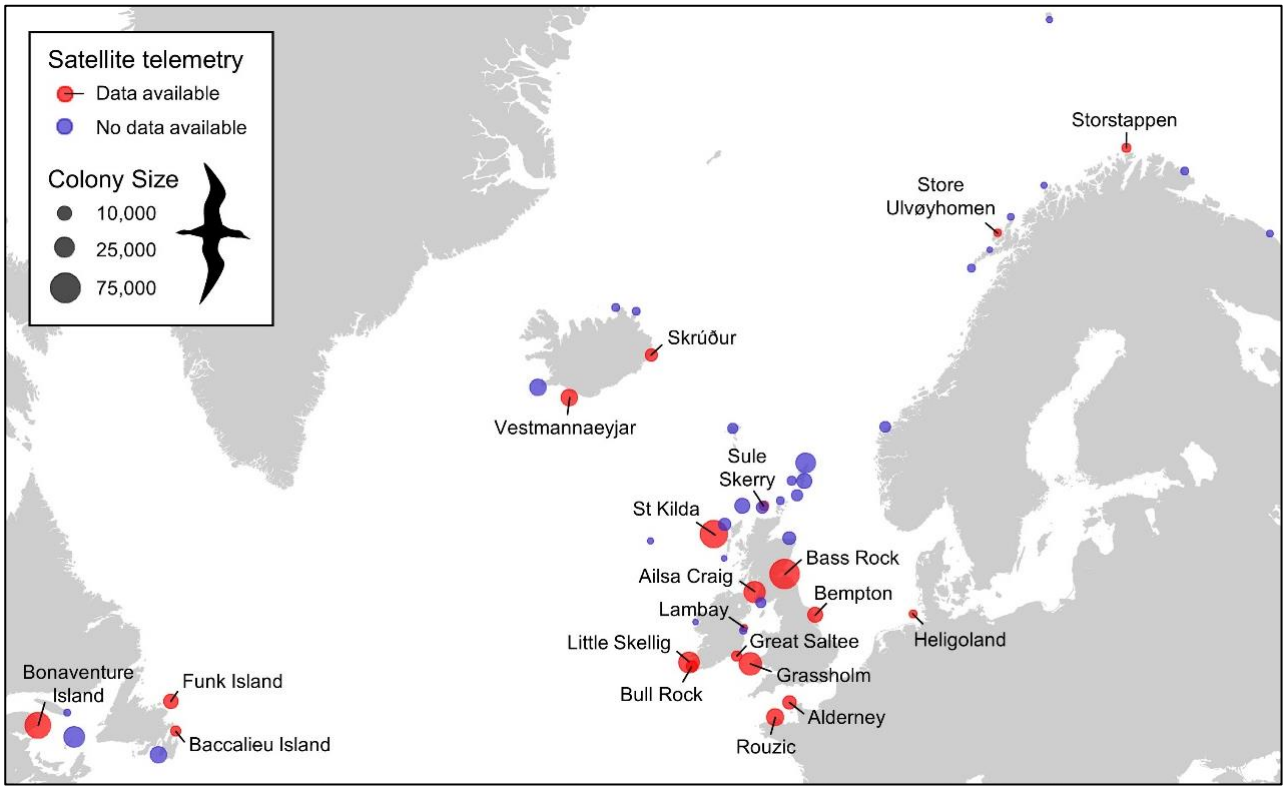


Figure 1.2. Northern gannet *Morus bassanus* colonies worldwide, adapted from Figure 6.1. Map adapted from tiles by Stamen Design, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

Table 1.1. Estimated numbers of breeding pairs of northern gannets *Morus bassanus* worldwide. Estimates for ~1910 are from Gurney (1913), 1914-1935 from Wynne Edwards *et al.* (1936), and 1996-2014 from Barrett *et al.* (2017), Chardine *et al.* (2013), Garðarsson (2019), Murray *et al.* (2015a) and the Joint Nature Conservation Committee Seabird Monitoring Program database.

Country	Colony	~1910	1914-1935	1996-2014
Scotland	Bass Rock	3,250	4,147	75,259
	St Kilda	15,000	16,500	60,290
	Ailsa Craig	3,250	7,000	33,226
	Hermaness	-	1,000	25,580
	Noss	-	800	11,786
	Sula Sgeir	4,000	5,000	11,230
	Sule Stack	4,000	4,000	1,870
	Nine other colonies	-	-	24,264
Canada	Bonaventure	3,500	6,500	59,586
	Bird Rocks	1,500	500	30,010
	Cape St. Mary	-	4,500	14,789
	Funk	-	-	9,987
	Baccalieu	-	-	2,253
	Anticosti	-	500	200
Ireland	Little Skellig	8,000	10,000	29,683
	Bull Rock	250	400	3,694
	Great Saltee	-	1	2,446
	Three other colonies	-	-	3,091
Iceland	Vestmannaeyjar	2,000	4,000	15,044
	Eldey & Geirfugladrangr	9,500	8,000	14,810
	Skrúður	-	-	6,051
	Grimsey	100	21	0
Wales	Grassholm	200	4,750	36,011
France	Rouzic	-	-	21,545
England	Bempton	-	-	11,061
Channel Islands	Alderney	-	-	7,885
Norway	Eight colonies	-	-	6,900
Faeroes	Myggenaes	750	750	2,340
Germany	Heligoland	-	-	656
Russia	Kharlov	-	-	241
Total		~50,500	~78,000	~522,000

Gannets are central place foragers in the breeding season, when they fly up to 590km from the colony to find food for themselves and their chick (Hamer *et al.,* 2007). Flight is the fastest but most energetically expensive mode of travel per unit time (Guigueno *et al.,* 2019). Many species, including other large seabirds, have adapted to make use of air currents to dramatically reduce their energetic expenditure. For example, the heart rate of wandering albatrosses *Diomedea exulans* flying with a favourable wind is almost the same as during resting (Weimerskirch *et al.,* 2000). Despite their large wingspan, gannets have not adapted to travel in this way. They have an energetically expensive mode of flight (Birt-Friesen *et al.,* 1989); the Cape gannet has a field metabolic rate of more than double that during flight than when resting (Green *et al.,* 2009). Gannets regularly glide and soar, but these behaviours only last a few seconds. However, Cape gannet heart rates change rapidly when switching between gliding/soaring and flapping flight, although the ~15% difference is small (Ropert-Coudert *et al.,* 2006).

On reaching a prey patch, gannets perform a specialised high-speed plunge dive from an average of ~37m above the water (Garthe *et al.,* 2014). Most dives are “v-shaped” plunge dives in which the bird returns to the surface quickly, to a depth of up to 10.4m, normally to ~4.5m (Cox *et al.,* 2016; Ropert-Coudert *et al.,* 2009). Accelerometry has revealed that gannets increase the length and depth of their dives using underwater wingbeats starting at 8.3m ± 0.8 SD depth, to reach ~14.5m ± 5.1 (Ropert-Coudert *et al.,* 2009). Once on the surface of the water, gannets must then take off and flap hard to regain altitude. As the diving and commuting costs for gannets are substantial, the foraging trip duration and the distances travelled are expected to be good indicators of overall foraging effort, but this has not been explored in detail.

1.5 Study sites: Grassholm, UK; Hellisey and Skrúður, Iceland

The primary field site for this thesis was Grassholm (51.73ºN, 5.48ºW), an offshore gannetry in Wales (Figure 1.3). Grassholm is the oldest RSPB-owned reserve having been purchased in 1947, and public landing is not permitted. The colony was first estimated at 250 nests in 1886 (Gurney, 1913) and like many other gannetries, has grown substantially, now being the third largest (Murray *et al.,* 2015a). Nesting gannets now use most of the land area on Grassholm, with 36,011 apparently occupied nests recorded in 2015 (Murray *et al.,* 2015b).

Gannets from Grassholm forage mainly in the Celtic Sea with some trips into the Irish Sea, Bristol Channel and English Channel (Waggitt *et al.,* 2014). Gannets sampled from different areas within the colony are representative of the colony as a whole as they have similar isotopic signatures and foraging trip distances, durations, directions and core foraging areas (Waggitt *et al.,* 2014). Gannets here feed on a range of different species, mainly mackerel *Scomber scombrus*, herring *Clupea harengus*, garfish *Belone belone* and fisheries discards (RSPB unpublished report, 2018). In 2011, 42% of the searching behaviour was associated with vessels (Votier *et al.,* 2013). Studying scavenging behaviour in the Celtic Sea is timely given that the 2015-19 reforms of the EU Common Fisheries Policy will reduce the fishery discards that subsidise the diets of gannets breeding in Europe (Commission of European Communities, 2009). Gannets have been studied on Grassholm since 2006, providing a long time series of data (Stauss *et al.,* 2012).

We also tracked gannets from two Icelandic colonies (Figure 1.4): Skrúður (64.90ºN, 13.63ºW) with 6,051 apparently occupied nest sites in 2013 and Hellisey (63.36ºN, 20.37ºW) with 3,374 in 2014 (Garðarsson, 2019). Hellisey is part of the Vestmannaeyjar archipelago, where gannets were recorded as far back as the 1750s (Gurney, 1913), while Skrúður is a newer colony, established in 1947 (Garthe *et al.,* 2016). The history of the gannet in Iceland is well-documented because the populations have been harvested. We collected the first gannet GPS tracking data for Iceland. Firstly, this allowed us to investigate how gannets interact with fisheries in a region with an active discard ban (Popsescu & Poulsen, 2012). This is key because most studies of seabird-fishery interactions take place in areas with high discarding rates (Soriano-Redondo *et al.,* 2016; Tew Kai *et al.,* 2013; Votier *et al.,* 2013). Secondly, this data filled a large gap in the latitudinal range of tracking studies between Sule Skerry in Scotland at 59.08ºN (Wakefield *et al.,* 2013) and Store Ulvøyhomen in Norway at 68.85ºN (Pettex *et al.,* 2012). By combining our new data with existing values, we could investigate gannet foraging behaviour across a large spatial gradient.

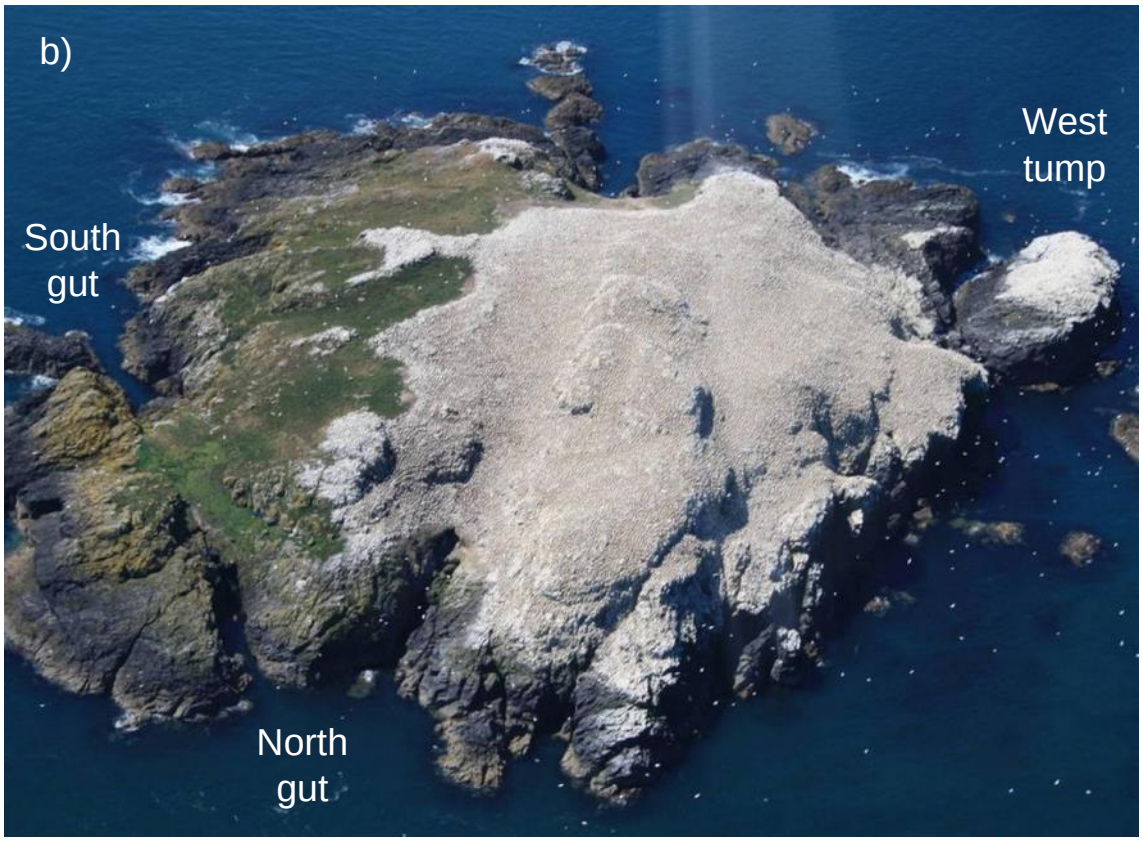


Figure 1.3. Grassholm Island gannet colony a) map from The Gannet: A bird with a history (Gurney, 1913); and b) ariel photograph taken by Stuart Murray in 2009.

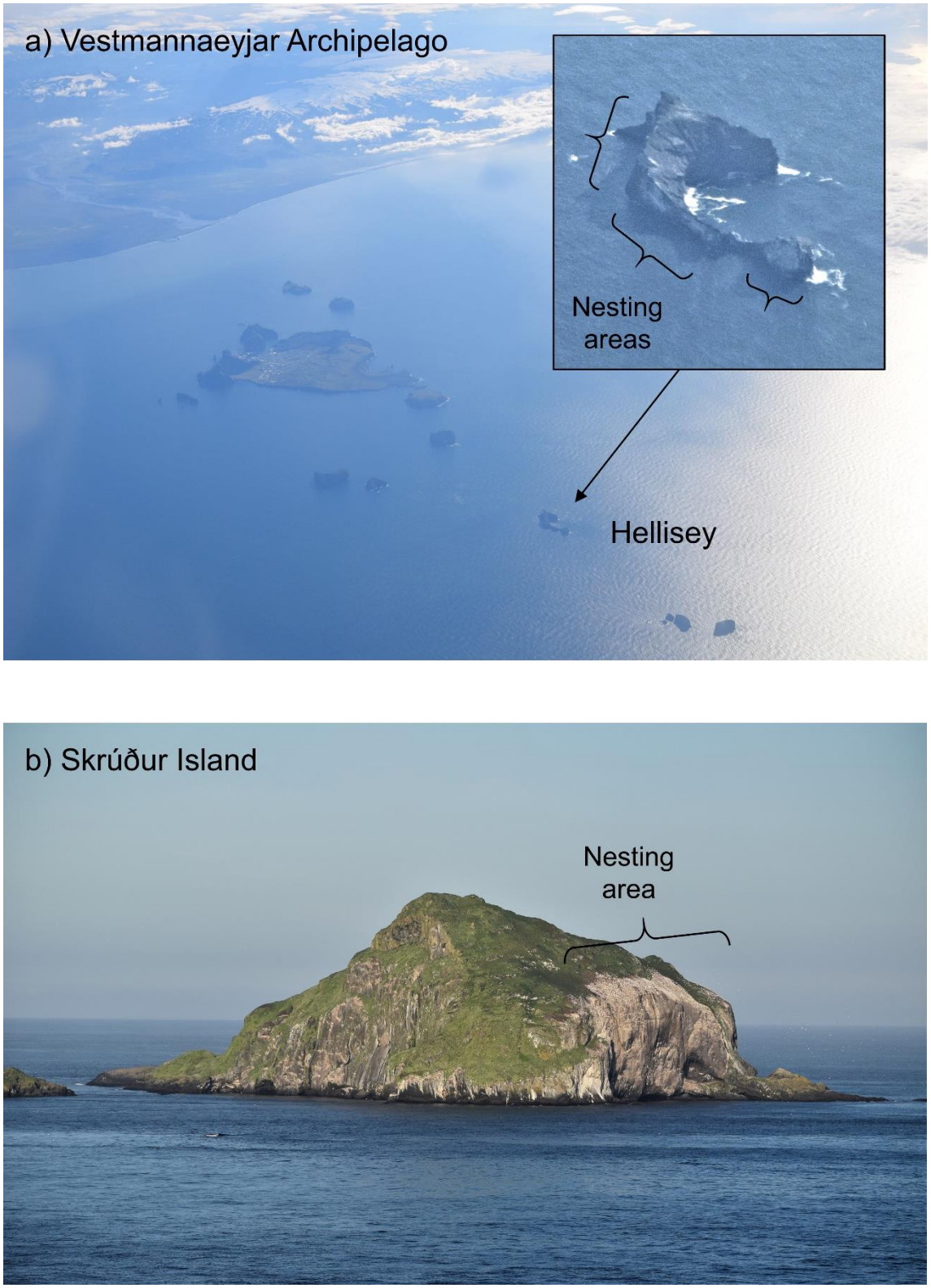


Figure 1.4. Photographs of a) Hellisey within the Vestmannaeyjar archipelago, and b) Skrúður showing the nesting areas of northern gannets, taken by B Clark.

1.6 Thesis outline

This thesis investigates the ecology and effort associated with foraging behaviour, using gannets as a study species. The five data chapters are outlined below.

Chapter 2 considers sexual segregation in gannet foraging and how this varies over an 11-year period in terms of foraging trip length, broad-scale space-use, fine-scale habitat selection, time of day and diet (measured by stable isotope analysis).

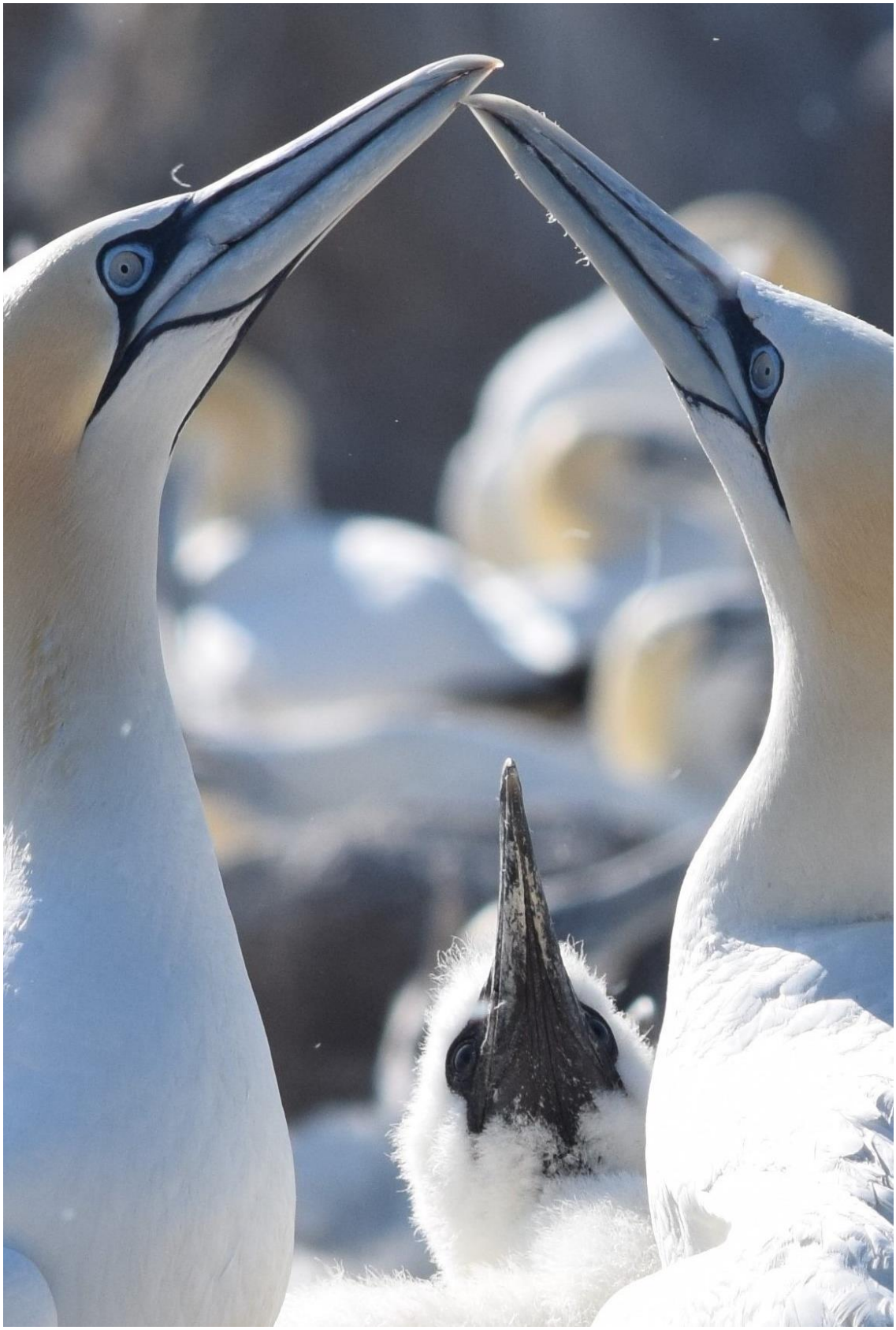
Chapter 3 examines foraging effort in greater detail. By combining GPS, acceleration and altitude data, I explore how the relative energetic costs of different behaviours relate to time spent, distance travelled and the gain or loss of altitude. Additionally, I test whether GPS-derived metrics are a good proxy for energetic expenditure.

Chapter 4 reveals the incidence of scavenging behaviour in gannets nesting on Grassholm using bird-borne video cameras, and describes how gannets not only feed on discards but also exploit vessels during hauling. This chapter then compares the relative behavioural patterns and energetic costs of scavenging and natural foraging.

Chapter 5 investigates the behavioural responses of gannets to fishing vessels in a region where discarding is banned, using GPS loggers and time-matched vessel locations. This data spans two Icelandic colonies across two years and provides a comparison to research carried out with the same methods in the Celtic Sea.

Chapter 6 relates foraging effort to latitude and colony size, and explores how this relationship may allow colonial species to shift their ranges in response to climate change. By utilising the large set of existing satellite tracking data for gannet foraging trips and combining that with tracks from Icelandic colonies, we have enough data to investigate these broad-scale questions.

Chapter 2 – Long-term patterns of sexual segregation in northern gannets *Morus bassanus*



2.1 Abstract

Sex-specific niche differentiation is common across a broad range of animals, but most studies examine this over short periods, and the persistence of such segregation is largely unknown. Here we investigate the interannual stability of sexual segregation among breeding northern gannets *Morus bassanus*, a wide-ranging, central-place forager with slight sexual dimorphism. Over 11 breeding seasons, we used GPS tracking and stable isotopes to test for sex differences in foraging trip range, duration and timing; spatial distribution; habitat selection; and carbon and nitrogen isotopes in blood. Across all years, female foraging trips were longer in duration and distance, yet, despite this, the foraging areas of males and females almost completely overlapped. Males and females selected foraging habitats that differed in terms of oceanography but not fishing vessel density. There was also evidence of temporal segregation: females were more likely to be at sea during the day, and males at night. Crucially, all these movement-based metrics varied interannually, with sex differences detected in some years but not others. Finally, we found that males had higher $\delta^{13}C$ and $\delta^{15}N$ than females in all years, indicating consistently distinct trophic niches. This is more likely to be a consequence of fine-scale habitat selection or temporal segregation than broad-scale space-use. Our results demonstrate clear sex differences in gannet foraging in some measures but not others, while strong interannual variation suggests this is influenced by environmental conditions. These results suggest that inferences drawn from single-year studies may not relate to general patterns, highlighting the importance of long-term studies.

Keywords: sex-specific behaviour, bio-logging, seabirds, central-place foraging, stable isotopes, northern gannet, *Morus bassanus*

2.2 Introduction

Male and female animals frequently occupy distinct foraging niches (Catry *et al.,* 2005; Mysterud, 2000; Wearmouth & Sims, 2008), hypothesised to be driven by a combination of competitive displacement and sex-specific specialisation (Catry *et al.,* 2005). Sex-specific foraging plays a major role in structuring the spatial and temporal distributions of species by reducing intraspecific competition (Catry *et al.,* 2005; González-Solís *et al.,* 2000), and allowing the sexes to differ in activity budgets or nutritional requirements related to their reproductive roles (Ruckstuhl & Neuhaus, 2002). Sex-specific niches can manifest in different ways, including in space, time, habitat use, diet and parental roles (Bernstein & Maxson, 1984; Breed *et al.,* 2006; Fraser *et al.,* 2002; Mysterud, 2000; Selander, 1966). The degree of sexual segregation can vary over time, both between breeding stages (Phillips *et al.,* 2004) and across the annual cycle (Castillo-Guerrero & Mellink, 2011; Besel *et al.,* 2018), but few studies examine this over long periods. Therefore, the persistence of such niche segregation is rarely known and needs to be addressed by multi-year studies in order to understand the causes and consequences of sexual segregation.

Seabirds are a useful model for studying sexual segregation as they are socially monogamous and share parental duties (Lack, 1968), restricting both sexes to the nesting colonies such that they compete during the breeding season. Studies have revealed sex difference in broad-scale space-use, fine-scale habitat use, activity patterns, diet and trophic position (Bearhop *et al.,* 2006; González-Solís *et al.,* 2000; Harris *et al.,* 2013). Such studies are generally conducted over short periods (1-3 breeding seasons; e.g. Becker *et al.,* 2007; Burke *et al.,* 2015; Elliott *et al.,* 2010; Paiva *et al.,* 2017; Woo *et al.,* 2009), with few examining long-term variability. Determining the extent to which sex differences are maintained over multiple years provides insight into the possible influence of extrinsic and intrinsic factors that underpin such differences.

Most studies of sexual segregation have focused on size dimorphic species (Phillips *et al.,* 2011; Ruckstuhl & Clutton-Brock, 2006), demonstrating that size differences explain variation in habitat selection and foraging behaviour (Ruckstuhl & Neuhaus, 2002; Selander, 1966; Wearmouth & Sims, 2008). However, monomorphic seabirds also segregate by sex (Hedd *et al.,* 2014; Thaxter *et al.,* 2009), and there is no evidence that the degree of size dimorphism between is linked to the degree of dietary segregation (Mancini *et al.,* 2013). The

mechanisms for sex-specific foraging in species where the sexes are broadly similar in size are often unclear, as males and females appear to have similar physical abilities to access prey. Differences may be linked to distinct parental roles in which males prioritise nest defence and females prioritise chick provisioning (Burger, 1981; Wojczulanis-Jakubas *et al.,* 2009). As such, considering behavioural sex differences without clear morphological differences promotes a greater understanding of the processes underlying sex-specific foraging.

Here, we investigate long-term patterns in the sex-specific foraging behaviour of a slightly dimorphic species, the northern gannet *Morus bassanus* (hereafter "gannet"). Previous research revealed sex differences over one to three breeding seasons in isotopic niche, departure direction, dive characteristics, foraging trip distance and duration, and habitat selection (Cox *et al.,* 2016; Cleasby *et al.,* 2015a; Lewis *et al.,* 2002, 2004; Stauss *et al.,* 2012). We used GPS tracking and stable isotopes to test for sex differences in trophic, spatial and temporal niches across 11 breeding seasons from 2006 to 2017. We aim to measure the stability of foraging niche differentiation between the sexes to provide insights into the drivers of sexual segregation whilst highlighting methodological considerations for similar studies.

2.3 Methods

2.3.1 Study site and sampling

Fieldwork took place on Grassholm Island, UK (51º43'N, 05º28'W), during the chick-rearing periods (late-June to August) of 11 breeding seasons (2006 and 2008–17, with GPS tracking in 2006 and 2010-17, and stable isotope sampling in 2006, 2008–14 and 2016). The colony held ~30,000 pairs during the study period (Deakin *et al.,* 2019; Murray *et al.,* 2015). Gannets were captured at the nest using a carbon fibre pole with a noose or crook during the changeover between partners so that chicks were not left unattended. We captured the outgoing parent to ensure that foraging trips began immediately after release. GPS loggers were attached to the lower back or central tail feathers with Tesa® 4651 cloth tape. In 2006, birds were equipped with Earth and Ocean Technology 'GPSlog' loggers (65g) set to record fixes every three minutes. In 2010–17, birds were equipped with Mobile Action Technology i-gotU GT-120 (18g) or GT-600 (35g) loggers. GPS loggers were set to record fixes were recorded every one or

two minutes. Individual consistency in the foraging trip destination and dive location of chick-rearing individuals means that tracking a single foraging trip is likely to be representative of that individual within years and, to a lesser extent, between years (Patrick *et al.,* 2014; Votier *et al.,* 2017). Studies have shown no effects of loggers weighing 20g, 30g or 70g on the foraging trip duration or body mass of chick-rearing gannets (Hamer *et al.,* 2009, 2007; Lewis *et al.,* 2002). A 1–2ml blood sample was taken from the tarsal vein using 23–25-gauge needles for stable isotope analysis and molecular sexing. We recorded mass to the nearest 50g, flattened wing chord length to the nearest 1cm, and bill length to feathering to the nearest 0.1mm. All procedures were carried out under licence from Natural Resources Wales (22478:OTH:SB:2010), the British Trust for Ornithology (BTO: A4257), the BTO Special Methods Panel and the UK Home Office (30/3065).

2.3.2 Foraging trip range and duration

We defined foraging trips as beginning and ending when individuals crossed a radius of 200m from the centre of the colony and excluded incomplete trips. We calculated foraging range (maximum Euclidean distance from the colony) using the 'geosphere' R package (Hijmans, 2017). Range and trip duration were Box-Cox transformed, then modelled as functions of sex, year (as a factor), mass and a sex:mass interaction using Linear Mixed-effects Models (LMM) in the 'lme4' R package (Bates *et al.,* 2014), with random intercepts for each individual. We present the models with the lowest Akaike Information Criterion corrected for finite sample sizes (AICc).

2.3.3 Spatial segregation

We used GPS locations to quantify the broad-scale spatial overlap of foraging trips between males and females for each year. We subsampled locations to the nearest two-minute interval and excluded locations within 6.8km of the colony, as gannets from Grassholm rest on the water in this area (Carter *et al.,* 2016). We projected locations onto a Lambert azimuthal equal-area projection centred around the colony and estimated 100% utilisation distributions (UD) for each year and sex with kernel density estimation in the 'adehabitatHR' R package (Calenge, 2006), using the bivariate normal kernel with a cell size of 500m and a smoothing parameter of 11km (chosen to reflect the mean area-restricted search scale for

foraging gannets of 9.1km ± 1.9; Hamer *et al.* 2009). We measured UD overlap using Bhattacharyya's affinity (BA), which uses the kernel density in 3D, as this is robust to outliers and takes into account the parts of the distributions that do not overlap as well as parts that do. BA ranges from 0 (no overlap) to 1 (total overlap) (Bhattacharyya, 1943; Fieberg & Kochanny, 2005). We tested for a significant difference between the observed BA and a null distribution generated from 1,000 randomisations of sex using the observed sex ratio of each year. P is defined as the proportion of randomised BAs that do not exceed the observed BA (See Breed *et al.,* 2006; Cleasby *et al.,* 2015a). As sample sizes varied between 29 trips (in 2006) and 203, we repeated the procedure with three random samples of 29 trips for 2010–17. Home range size was estimated in km^2 using the 95% utilisation distribution (because home range size is more affected by outliers than BA overlap), and was then Box-Cox transformed and analysed using a Linear Model in R with sex and number of trips fitted as fixed effects. We calculated 25% UDs to visualise core use areas.

2.3.4 Habitat selection

We tested whether foraging habitat use differed between the sexes as a function of four candidate covariates: sea surface temperature, chlorophyll-a, thermal fronts and fishing vessel density. We included sea surface temperature and chlorophyll-a as male gannets from some colonies are more likely to use warmer areas with higher productivity than females (Cleasby *et al.,* 2015a). We included thermal fronts as gannets are more likely to perform area-restricted searching behaviour and dive in areas of seasonally persistent fronts (Cox *et al.,* 2016; Scales *et al.,* 2014), and the response to fronts can differ with sex (Cox *et al.,* 2016). Fishing vessel locations were included as gannets scavenge at fishing boats (Votier *et al.,* 2010, 2013; Bodey *et al.,* 2014), with some evidence that males scavenge more than females (Stauss *et al.,* 2012; Votier *et al.,* 2013), although other studies suggest no sex-specific differences in terms of scavenging (Patrick *et al.,* 2015). The Natural Environment Research Council Earth Observation Data Acquisition and Analysis Service (NEODAAS) supplied data for chlorophyll-a concentration (Aqua-MODIS & Suomi-VIIRS; see Gohin, Druon & Lampert, 2002), sea surface temperature (AVHRR; see Miller *et al.,* 1997) and thermal fronts (see Miller 2009) in a 1x1km grid. Habitat data were composites for the month of July (when the majority of the data were collected) to provide

sufficient cloud-free time. To reduce noise from non-persistent transient features, front composites combined the gradient, persistence and proximity of fronts over this one-month period (see Suberg *et al.,* 2019). This combined front metric facilitated the analysis by reducing the number of variables input to the habitat models. Vessel Monitoring System (VMS) data, on the density of vessels ≥15m, was obtained for three years (2005–07) in a 3x3km grid for vessels travelling at speeds of 3–10km per hour, which indicates fishing activity (Witt & Godley, 2007). Witt and Godley (2007) found that fisheries activity hotspots were consistent over five years (2000–04). To account for very high vessel densities near ports, we calculated the maximum vessel density in the study area more than 5km from the coast, and then excluded values exceeding this maximum within 5km of the coast (Witt & Godley, 2007).

We modelled selection by comparing the habitat at foraging locations with the available habitat (Aarts *et al.,* 2008). We first subsampled GPS data to two-minute intervals and extracted foraging locations based on speed, acceleration and tortuosity thresholds (see Wakefield *et al.,* 2013; Bennison *et al.,* 2017). For each foraging location, we generated 20 pseudo-absences within the 100% minimum convex polygon for all years (we did not use the 100% utilisation distribution calculated from the kernel density as this results in separated areas when gannets could forage in between). We removed locations with missing environmental data and then randomly sampled three for each foraging location (due to limited computing power). We first fitted binomial Generalised Additive Models (GAMs; 'gamm4' R package; Wood & Scheipl, 2017) with a logit link to model the presence/pseudo-absence of foraging locations in relation to each of the habitat variables (sea surface temperature, chlorophyll, thermal fronts, and vessel density), sex and the interaction between habitat and sex. To account for spatial autocorrelation, we used residuals autocovariate (RAC) models (Crase *et al.,* 2014, 2012; Escalle *et al.,* 2016). To do this, we extracted residuals from a fully fitted GAM to create a gridded raster of the spatial autocorrelation between neighbouring cells (based on a mean focal operation for a first order neighbourhood) using the 'raster' R package (Hijmans, 2018). We extracted the corresponding RA value for each presence/pseudo-absence location and then re-fitted a GAM including the generated RAC as a smooth term (cubic regression spline) with the number of knots chosen automatically through cross-validation (with no limit). We fitted a model for each habitat variable (models with all habitat

variables failed to converge due to memory and processing limits) to illustrate the overall pattern, and separate models for each year (2006 & 2010–16) to investigate interannual variation. We did not have oceanographic variables for 2017. Models were assessed using Cohen's kappa, the area under the receiver operating characteristic curve (ROC), and the Boyce index (Boyce *et al.,* 2002; Hirzel *et al.,* 2006).

2.3.5 Diel segregation

To test whether male and female foraging trips differed with the time of day, we extracted the times of at-sea locations during foraging trips at a 30-minute resolution. We analysed the timestamps using the 'overlap' R package designed for quantifying the overlap in diel cycles (Ridout & Linkie, 2009). Using this package, we calculated kernel density estimates from the timestamps, with the time of day treated as a circular variable such that 23:59 is 1 minute before 00:00. We tested the overlap between males and females by combining the data for all years, and separately for each year. We quantified the overlap using the $\hat{\Delta}_4$ coefficient of overlap (0 = no overlap, 1 = total overlap) and estimated 95% confidence intervals by bootstrapping with 10,000 resamples (Linkie & Ridout, 2011).

2.3.6 Isotopic segregation

To test for sex differences in diet, we measured stable isotope ratios in red blood cells (which have a turnover of 4–6 weeks; Rodnan *et al.,* 1957). Blood samples collected in nine years (2006, 2008–14 and 2016) were centrifuged to separate red blood cells from plasma. Red blood cells were freeze-dried and homogenised into a fine powder, and 0.7mg ± 0.1 was weighed into tin capsules. Analysis took place at the National Environment Research Council Life Sciences Mass Spectrometry Facility in East Kilbride, or the University of Exeter facility at the Environment and Sustainability Institute in Penryn. Results for isotope ratios of carbon $^{13}C/^{12}C$ and nitrogen $^{15}N/^{14}N$ are expressed as delta (δ) units, as parts per thousand (0/00) difference from international standards (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). Using Linear Models, we modelled stable isotope values for $\delta^{13}C$ and $\delta^{15}N$ in response to sex, year (treated as a factor), mass (as females are 6.8% heavier than males, with no difference in bill or tarsus length; Table S2.1), and the interaction between sex and mass.

2.4 Results

2.4.1 Foraging trip range and duration

We recorded 645,620 GPS locations during 634 complete foraging trips from 138 female and 159 male gannets across nine breeding seasons. Females undertook trips with greater foraging range and trip duration, controlling for mass (Table 2.1). Mean ± standard error foraging trip range was 107km ± 4 for males and 129km ± 5 for females, with a mean trip duration of 20.1 hours ± 0.8 for males and 24.2 hours ± 1.2 for females (Figure 2.1, Tables S2.2–S2.3). Heavier individuals of both sexes made shorter trips (Table S2.3). Foraging range and duration both varied with year, but there were no significant year:sex interactions (Table 2.1, Figure 2.1).

Table 2.1. Top candidate Linear Mixed Models to explain gannet foraging trip range and duration as a function of sex, year and mass, with individual as a random effect.

Model		AICc	Δ AICc	AICc weights	Deviance	Resid. df
Range ~	sex + year + mass + sex:mass	1051.2	-	0.564	1022.4	497
	sex + year + mass	1052.0	0.78	0.383	1025.2	498
	sex + year	1057.9	6.69	0.020	1033.3	499
Duration ~	sex + year + mass	378.5	-	0.659	351.7	498
	sex + year + mass + sex:mass	379.9	1.40	0.327	351.0	497
	sex + year	387.5	9.05	0.007	362.9	499

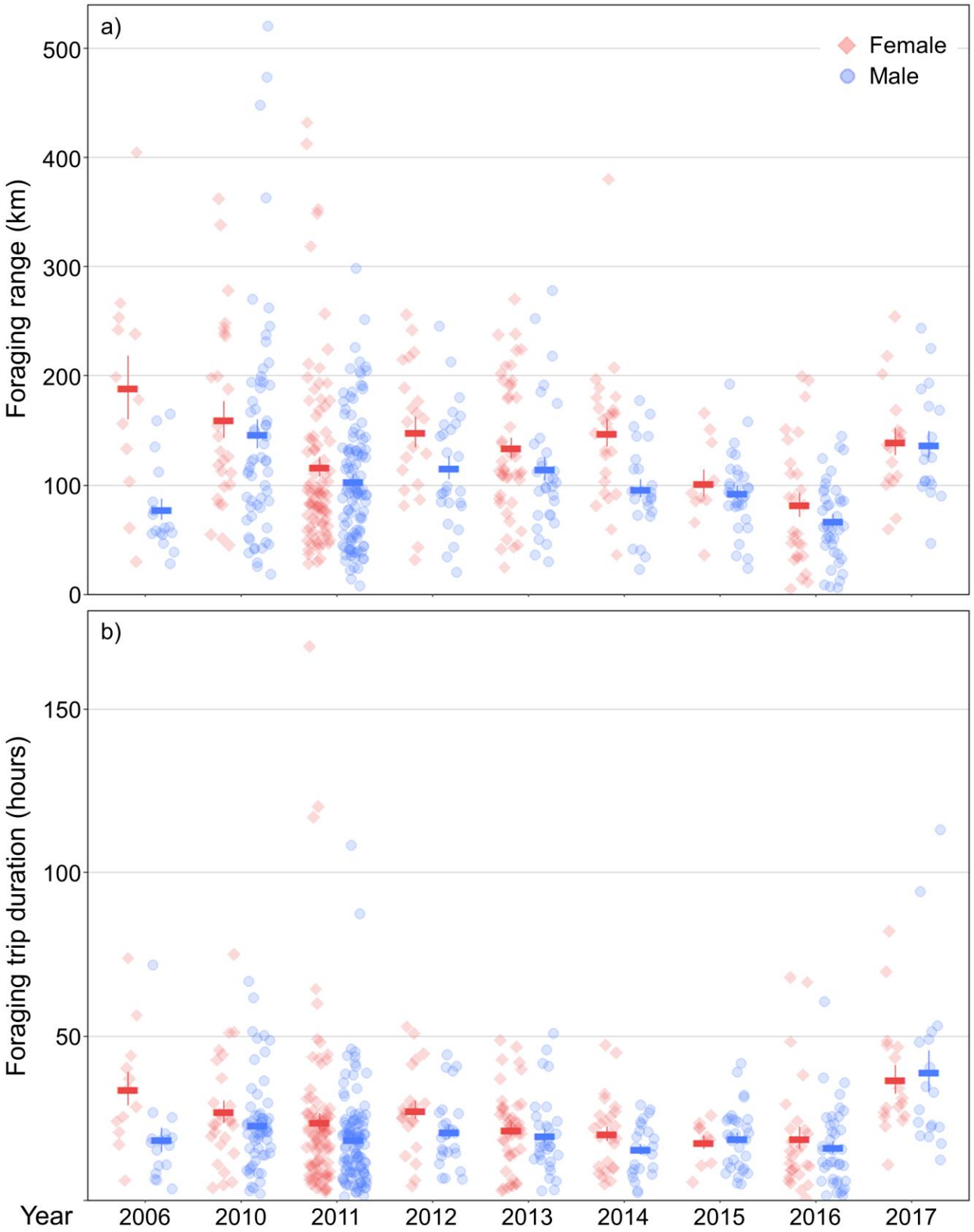


Figure 2.1. Foraging trip a) range (maximum distance from the colony) and b) duration for 138 female (red diamond, n = 272 trips) and 159 male (blue circle, n = 362 trips) chick-rearing gannets on Grassholm Island, UK. Bars show annual means ± SE and jittered points show individual trips.

2.4.2 Spatial segregation

There was no difference in home range size across all years (Figure 2.2; LM, $F_{2,15}$ = 1.54, p = 0.234), but the home range was slightly larger for females in some years and males in others (Table S2.2, Figure 2.3), with a substantial difference in 2006 (223% larger for females). When the data from all years were combined, the 100% UDs for males and females were not significantly different (BA overlap = 0.92, P = 0.087; Figure 2.2). There was, however, interannual variation (Figure 2.3), with significant segregation occurring in 2006 (BA = 0.432, P = 0.004) and 2013 (BA = 0.798, P = 0.022). As the sample size was smallest in 2006 (29 trips), we took three random sub-samples of 29 trips for years 2010-2017. These produced lower BA values, but no significant segregation was detected (Table S2.4), indicating that the segregation detected in 2006 was not a result of the smaller number of recorded trips.

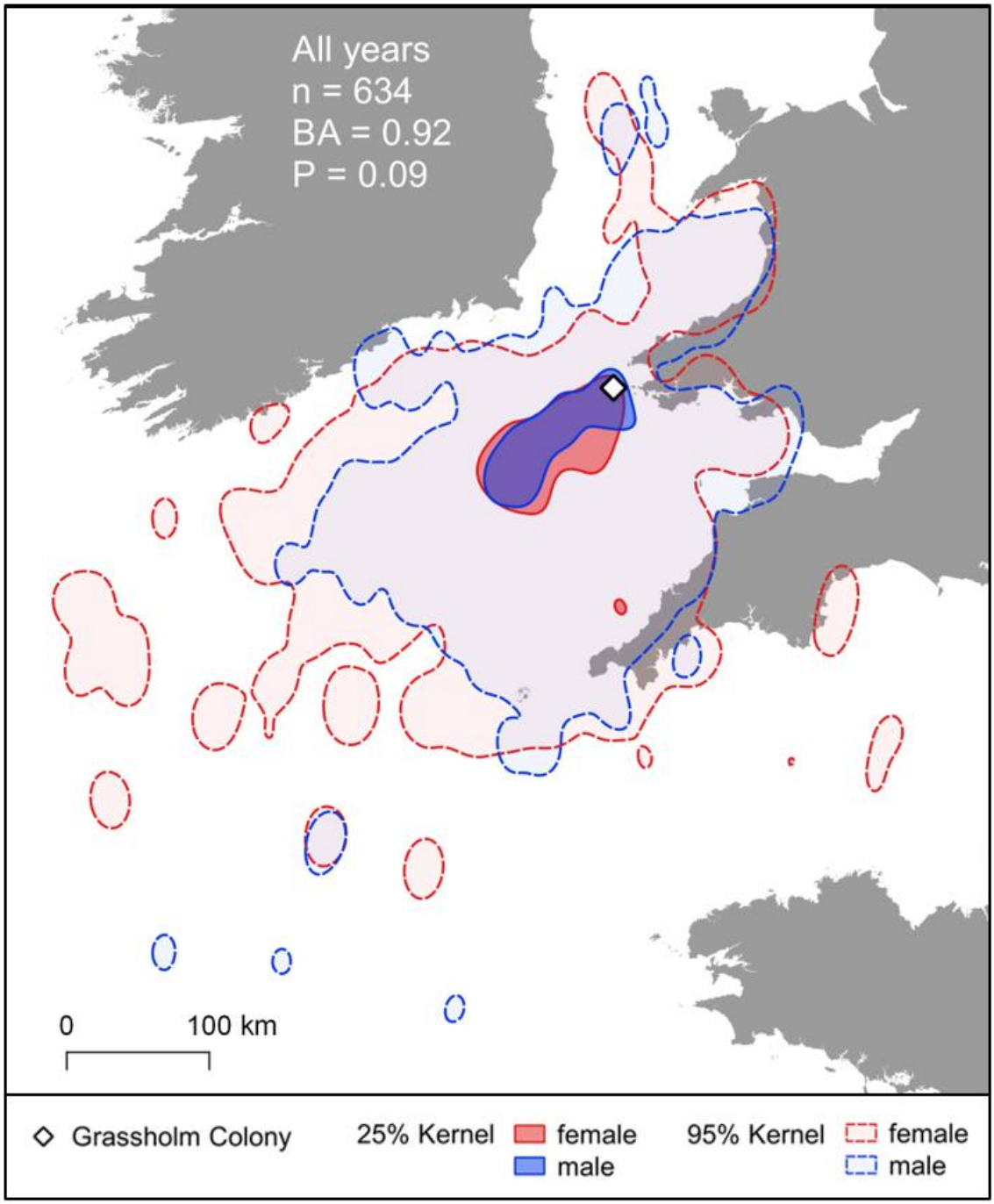


Figure 2.2. Home ranges (95% utilisation distribution (UD) and core areas (25% UD) for female (red) and male (blue) northern gannets *Morus bassanus* GPS-tracked from Grassholm Island, UK, combined across 2006 and 2010-17. BA (Bhattacharyya's affinity) = Estimated overlap between male and female 100% UDs. P = Proportion of simulated BAs that did not exceed the observed BA. n = number of trips. *P < 0.05, **P < 0.01.

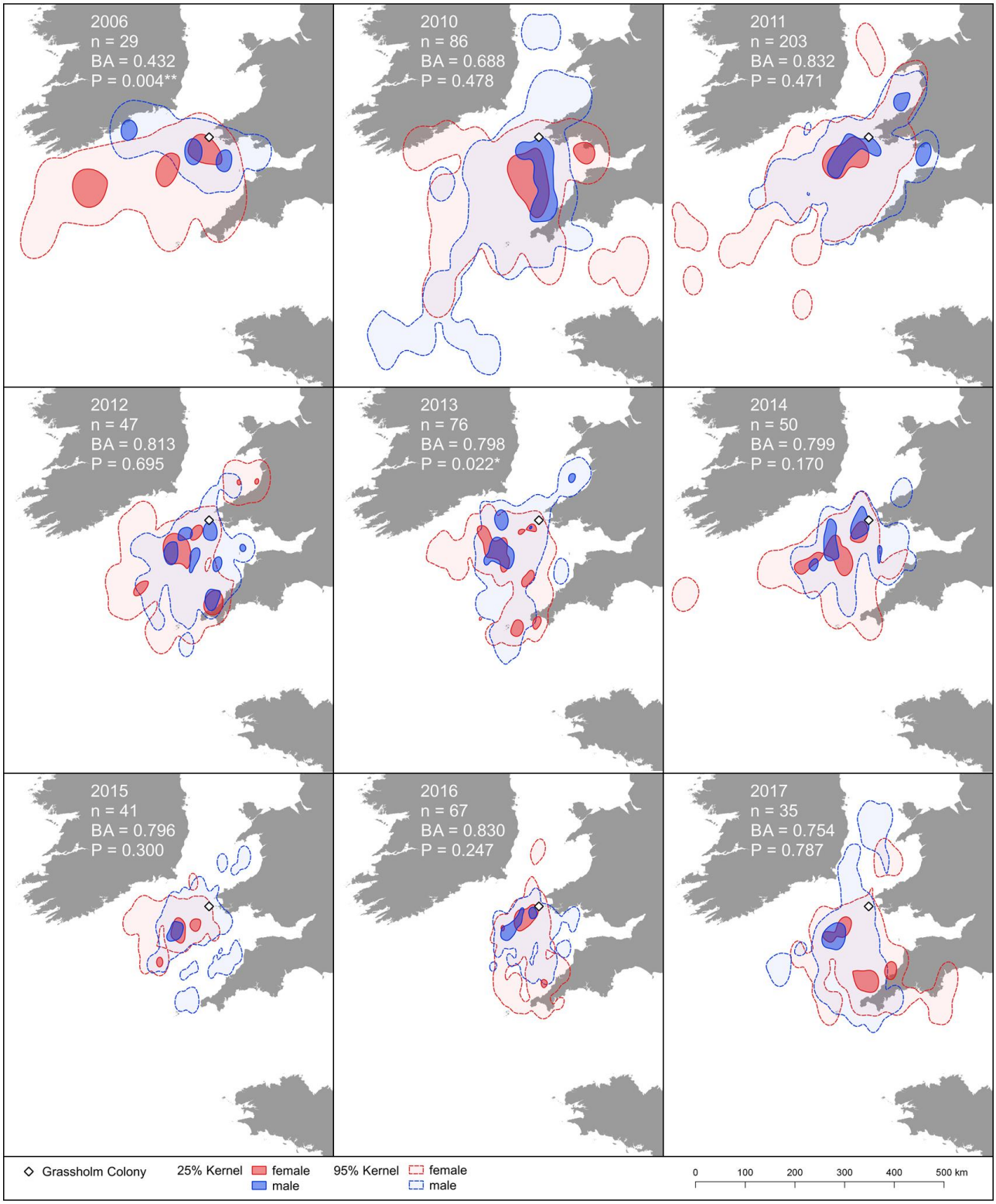


Figure 2.3. Annual home ranges (95% utilisation distribution (UD) and core areas (25% UD) for female (red) and male (blue) northern gannets *Morus bassanus* GPS-tracked from Grassholm Island, Wales, UK. BA (Bhattacharyya's affinity) = Estimated overlap between male and female 100% UDs. P = Proportion of simulated BAs that did not exceed the observed BA. n = number of trips. *P < 0.05, **P < 0.01.

2.4.3 Habitat selection

Male and female gannets differed in their habitat selection (Table 2.2), but this was highly variable between years (Figure 2.4; Tables S2.5–S2.6). Generally, females made greater use of locations with lower sea surface temperatures, lower chlorophyll-a concentrations and higher composite thermal front intensity (combined strength, persistence and proximity) than males. The model for chlorophyll-a in 2011 failed to converge. However, there was no sex-specific selection for the density of fishing vessel activity (number of VMS records at fishing speed).

Table 2.2. Estimates for the effect of an interaction between the habitat variable and sex on the probability of a location being a gannet foraging location or a pseudo-absence (**p<0.01, ***p<0.001). Delta (Δ) AIC refers to the change in AIC caused by removing the interaction.

Habitat variable	Estimate for sex interaction	p value	Δ AIC
Sea surface temperature	-0.349	<0.001 ***	34.05
Chlorophyll-a concentration	0.601	<0.001 ***	78.64
Thermal front levels	0.113	0.006 **	5.39
Vessel density	0.055	0.295	-0.90

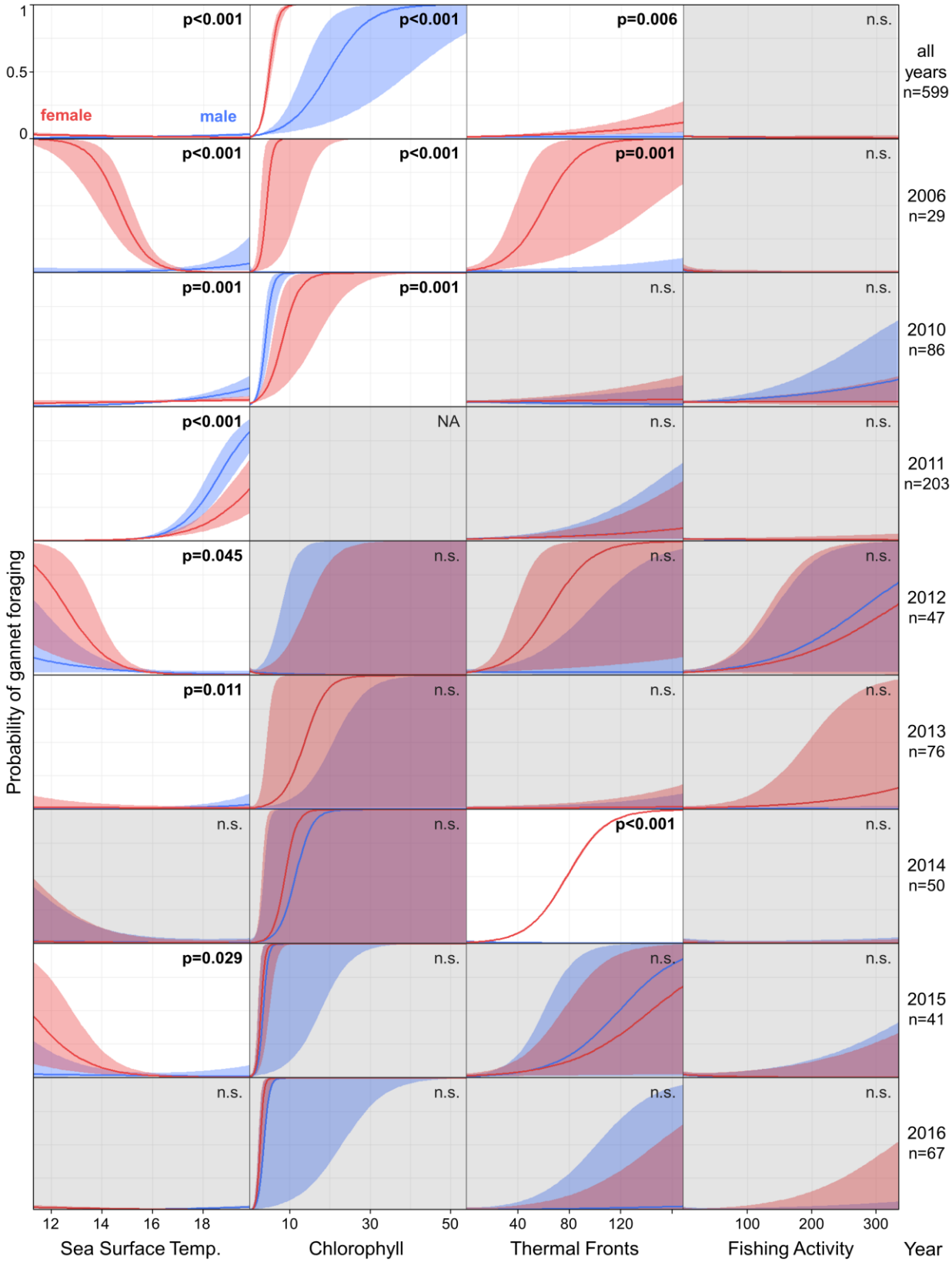


Figure 2.4. Habitat selection for female (red) and male (blue) gannets *Morus bassanus* over eight breeding seasons. Probability of locations being a foraging event rather than a pseudo-absence in response to sea surface temperature (°C), chlorophyll-a concentration, thermal fronts (strength, persistence and proximity) and fishing vessel density. Ribbons represent 95% confidence intervals. p = p-value of the sex:habitat interaction. n.s. = p>0.05 (grey background). n = number of trips.

2.4.4 Diel segregation

Male and female gannet at-sea locations broadly overlapped in their time of day, but the bootstrapped upper 95% confidence interval (CI) indicate temporal segregation (across all years: $\hat{\Delta}_4$ coefficient of overlap = 0.970, 95% CI = 0.960-0.980). Males were more likely to have foraging trips that include an overnight component, while females were more likely to be away from the colony during the day (Figure 2.5). This effect was detected within 7 of the 9 years studied.

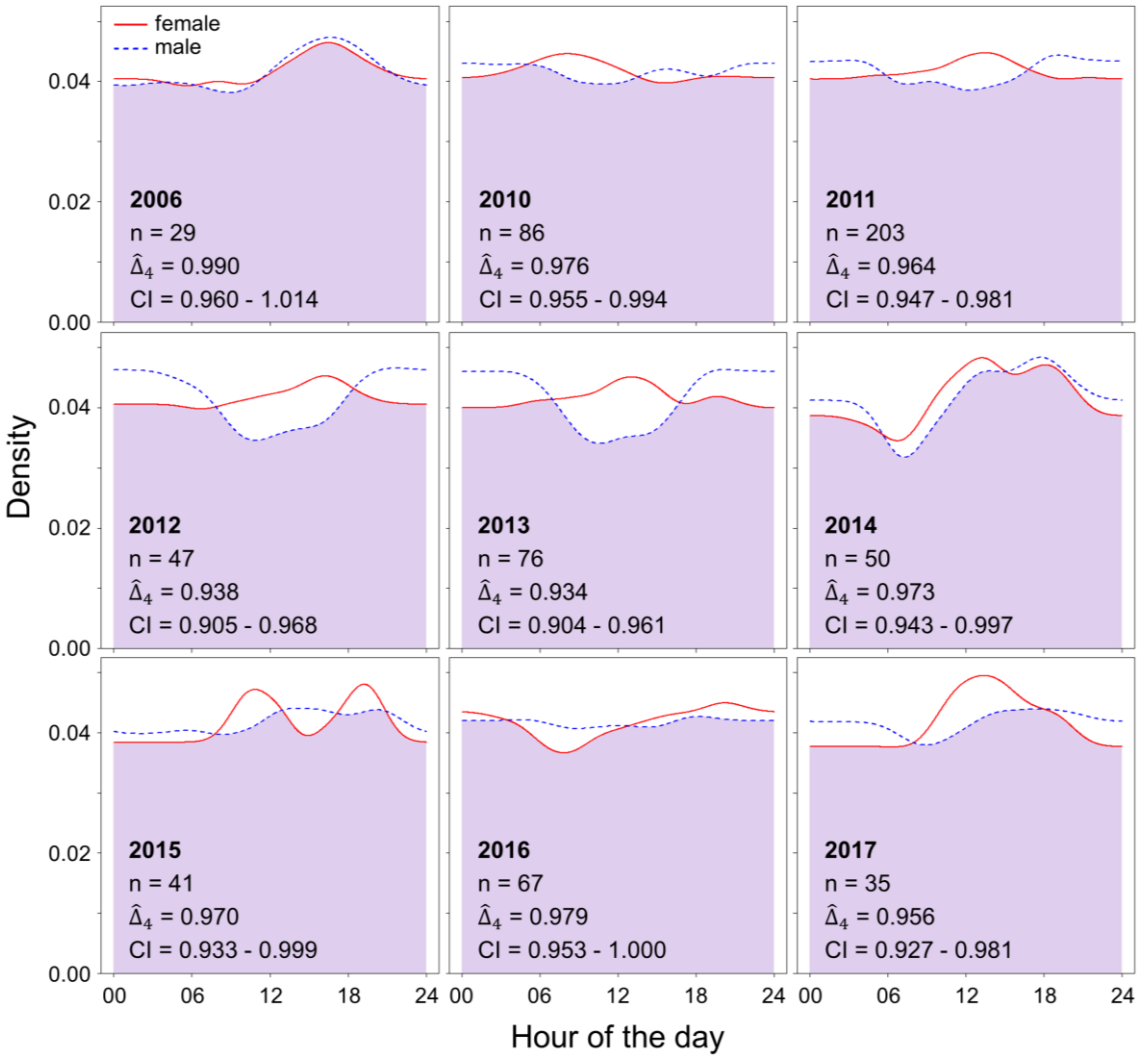


Figure 2.5. Density of at-sea locations across the hours of the day for female (red) and male (blue) northern gannets *Morus bassanus* GPS-tracked from Grassholm, Wales, during the breeding seasons of 2006, 2010–17. Purple shading indicates the overlap between sexes. n = number of trips. $\hat{\Delta}_4$ = the coefficient of overlap. CI = bootstrapped 95% confidence interval (CIs crossing 1 indicates that no difference is detected).

2.4.5 Isotopic segregation

Stable isotope values for $\delta^{13}C$ and $\delta^{15}N$ were significantly different between the sexes and were also significantly associated with year and mass (Table 2.3). There was a sex:year interaction for $\delta^{13}C$, with overlap in 2010 and 2013 (Table 2.3), but females still had lower mean $\delta^{13}C$ than males in all years of the study (Figure 2.6, Tables S2.7–S2.8). There was no sex:year interaction for $\delta^{15}N$, and errors overlap only in 2010 (Figure 2.6). The best models for $\delta^{13}C$ and $\delta^{15}N$ also contained a sex:mass interaction, although this was within 2 Δ AICc units of the model without the interaction for $\delta^{15}N$ (Table 2.3, Figure 2.7). Values for $\delta^{13}C$ were significantly lower for females than males, and values increased with mass for females (the heavier sex), but not for males (Table 2.3, Figure 2.7).

Table 2.3. Top candidate Linear Models to explain $\delta^{13}C$ and $\delta^{15}N$ stable isotope values.

Model		AICc	Δ AICc	AICc weights	Resid. deviance	Resid. d.f.
$\delta^{13}C$ ~	sex + year + mass + sex:year + sex:mass	433.1	-	0.586	62.52	314
	sex + year + mass + sex:year	435.2	2.09	0.206	63.34	315
	sex + year + mass	436.8	3.66	0.094	67.11	323
$\delta^{15}N$ ~	sex + year + mass + sex:mass	577.3	-	0.393	101.54	322
	sex + year + mass	577.4	0.09	0.375	102.23	323
	sex + year	579.6	2.31	0.124	103.58	324

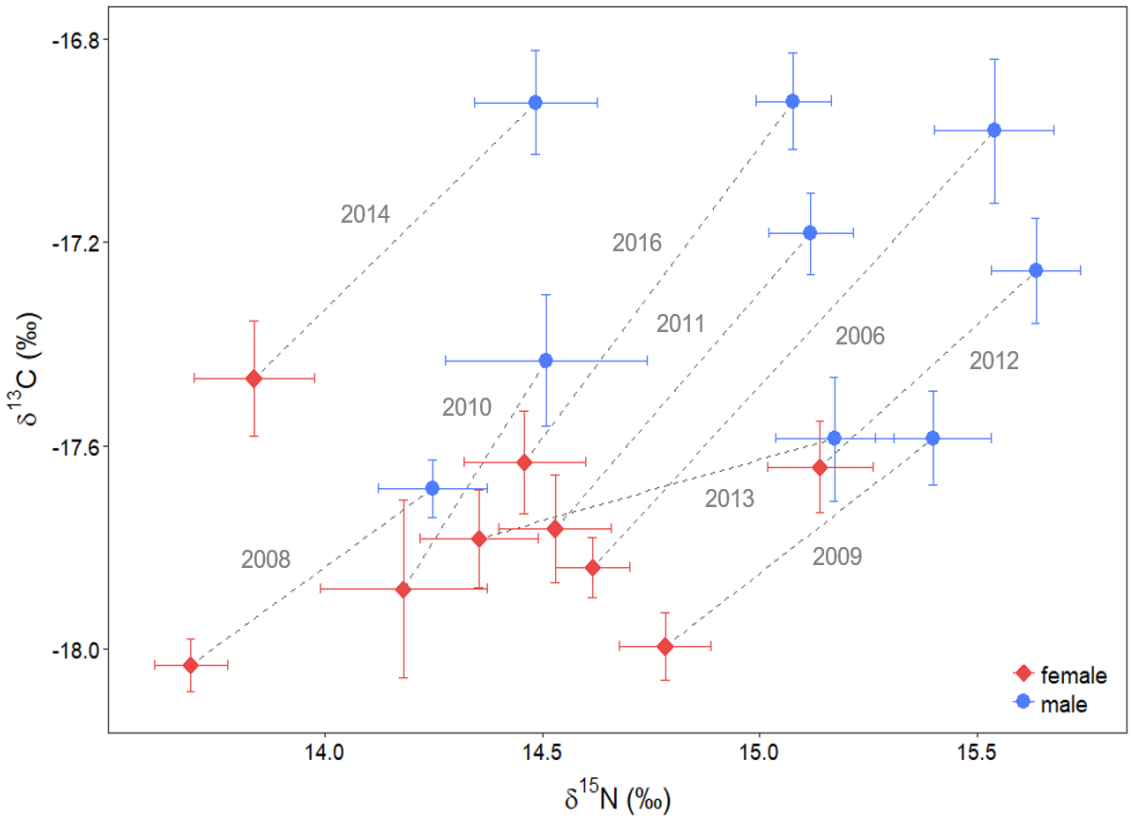


Figure 2.6. Mean stable carbon and nitrogen isotope values ± standard error derived from red blood cells for 168 female (red diamond) and 193 male (blue circle) northern gannets *Morus bassanus* from Grassholm, UK (2006, 2008–14 and 2016). Dashed lines indicate that values are from the same year.

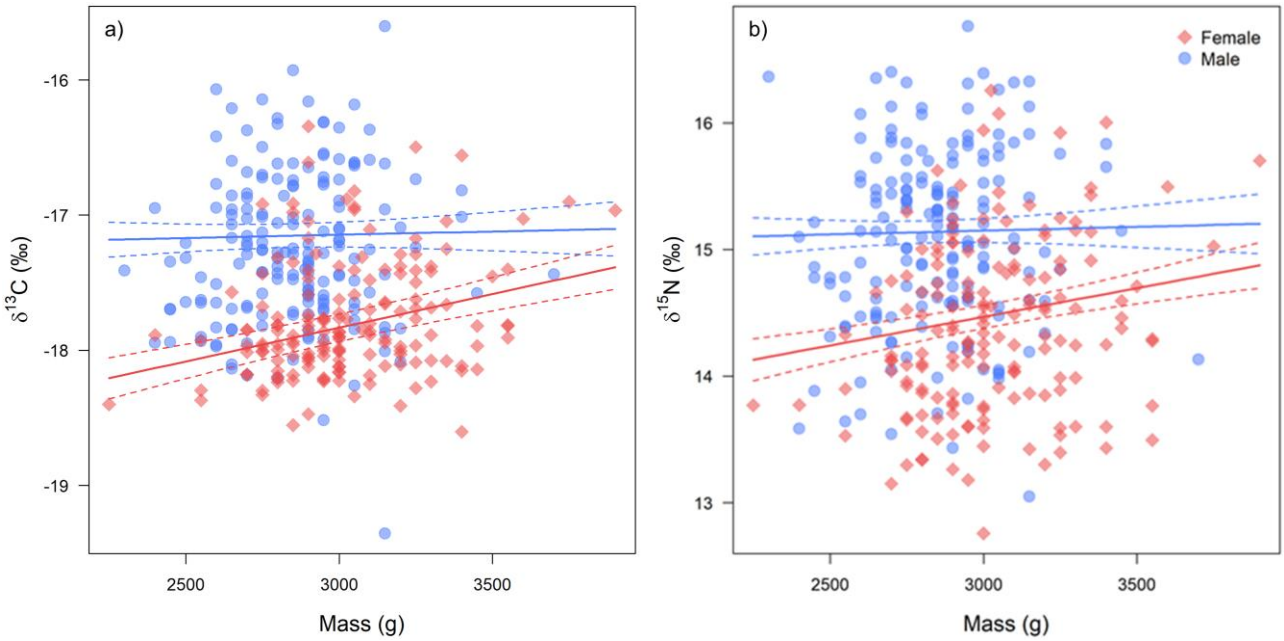


Figure 2.7. Stable isotope values for a) carbon ($\delta^{13}C$) and b) nitrogen ($\delta^{15}N$) in relation to body mass derived from red blood cells for female (red diamond) and male (blue circle) northern gannets *Morus bassanus* from Grassholm, UK, collected during the breeding seasons of 2006, 2008–14 and 2016. (Solid lines = model predictions, dashed = SE).

2.5 Discussion

By combining high-resolution GPS data with stable isotope analysis, we show that, despite overlap in broad-scale space use, breeding male and female gannets differ in terms of their foraging niche as characterised by foraging trip range, duration and timing, fine-scale habitat selection and isotopic niche. Importantly, these sex differences varied over the 11 years studied in terms of trip range, duration, habitat selection, timing and space use, while remaining consistent in isotopic niche.

2.5.1 Foraging trip distance and duration

Overall, females spent 20% more time on foraging trips and reached distances 21% further from the colony than males, although both measures varied among years (Figure 2.1; Table 2.1). Seabirds of the larger sex generally make shorter foraging trips (González-Solís *et al.,* 2000; Lewis *et al.,* 2005; Weimerskirch *et al.,* 1997). However, female gannets are slightly heavier than males (Table S2.1), and heavier individuals within each sex made shorter trips, showing that the isotopic segregation related to sex is not due to size dimorphism (Table 2.1). These observed differences could arise through competitive exclusion if males return to the colony earlier than females to defend the nest site (Kokko, 1999; Nelson, 1965), and occupy foraging areas closest to the colony, forcing females to travel further afield to avoid competition. However, male gannets do not always arrive earlier (Fifield *et al.,* 2014), or winter significantly closer to the colony (Fifield *et al.,* 2014; Kubetzki *et al.,* 2009; Stauss *et al.,* 2012; but see Deakin *et al.,* 2019). Alternatively, sex differences in trip length could reflect females investing more in foraging, while males invest more in nest defence (Burger, 1981). Sex differences varied among years (Figure 2.1), suggesting extrinsic factors such as variation in food availability may be involved, as observed in other seabird species (Castillo-Guerrero & Mellink, 2011; Paiva *et al.,* 2017; Ishikawa & Watanuki, 2002; Gladbach *et al.,* 2009). However, prey shortages can lead to diverging foraging effort (Botha *et al.,* 2017) or more equal provisioning rates (Fraser *et al.,* 2002). As such, more work is required to determine the drivers of interannual variation in sex-specific foraging effort.

2.5.2 Spatial segregation

In general, the foraging areas of males and females overlapped despite differences in foraging trip range and duration, which reflects the fairly even distribution of the additional area used by females around the area used by males (Figures 2.1–2.3). However, this was not consistent across all nine years, as we detected significant spatial segregation in 2006 and 2013 (Figure 2.3), with females ranging further than males in 2006. For gannets breeding at Bass Rock, SE Scotland, sex-specific foraging areas were observed in all three breeding seasons studied with females making longer trips (Cleasby *et al.,* 2015a), indicating variation between sites as well as between years. The difference between the colonies may be caused by higher levels of competition, as Bass Rock is a larger colony (~60,000 pairs at the time of the study, compared to ~30,000 for Grassholm; Murray *et al.,* 2015a), with differences in coastal morphology resulting in less available sea areas within the foraging range (Cleasby *et al.,* 2015a). Inter-colony variation was also observed for wandering albatrosses *Diomedea exulans*, which exhibit broad-scale spatial sexual segregation at some sites (Åkesson & Weimerskirch, 2014; Weimerskirch *et al.,* 2012), but not others (Pereira *et al.,* 2018; Xavier *et al.,* 2004). These patterns indicate that the extent of spatial segregation is not fixed but relates to differences in how males and females respond to environmental conditions.

2.5.3 Habitat selection

Like wandering albatrosses (Pereira *et al.,* 2018), gannets exhibited sex-specific habitat-selection despite large-scale spatial overlap (Figures 2.2–2.4). Males and females selected waters with differing sea surface temperatures (SST), chlorophyll-a concentrations and composite thermal fronts. There were no sex differences in response to fishing vessel density in any year (Figure 2.4), but this may be because the vessel data was not temporally matched to the gannet tracking data. However, we detected significant sex-habitat interactions for SST in six years (not 2014 or 2016), chlorophyll-a in only 2006 and 2010, and thermal fronts in only 2006 and 2014. Females consistently preferred lower SST and higher composite thermal fronts (combined gradient, persistence and proximity). However, for chlorophyll-a, females selected areas with high concentrations in 2006, while males selected areas with high concentrations in 2010. We detected a sex interaction with all oceanographic indices only in 2006, when there was

substantial spatial segregation, suggesting that the two are linked. Overall, responses to the habitat variables measured in our study were highly changeable, which may be explained by the sample of individuals tracked each year and/or by interannual variation in local conditions. Individual gannets may have specific habitat types or foraging specialisms (such as scavenging from fishing vessels; Votier *et al.,* 2013), with competitive pressure leading to a diversity of strategies, where the likelihood of choosing a particular specialism may or may not relate to sex. Furthermore, most individual gannets are repeatable in their foraging areas (Patrick *et al.,* 2014; Votier *et al.,* 2017; Wakefield *et al.,* 2015), and so differences in sex-specific behaviour may occur due to changes in the underlying habitat if individuals are more faithful to geographic space than habitat types.

2.5.4 Diel segregation

There were slight sex differences in the timing of foraging trips; males were more likely to be at sea overnight and females during the day (Figure 2.5), as observed in other sulids (Botha *et al.,* 2017; Miller *et al.,* 2018). As such, males were more likely to have trips with an overnight component when they cannot forage, despite having shorter trips than females. This pattern may be driven by higher investment from males in nest defence from largely diurnal conspecifics and predators (e.g. great black-backed gulls *Larus marinus;* Garthe & Huppop, 1996), making them more likely to be at the colony during daylight hours (Burger, 1981; Fifield *et al.,* 2014). Diel segregation could also reduce intraspecific competition (Bernstein & Maxson, 1984), including between sexes (Elliott & Gaston, 2015). Sex-specific timing of foraging in imperial shags *Phalacrocorax atriceps* occurred only during the breeding season, suggesting that this is driven by the constraint of competition or attending the nest rather than foraging specialisation (Harris *et al.,* 2013).

Diel cycles can impact diet as fish tend to inhabit deeper waters during daylight to avoid visual predators (Gliwicz, 1986; Wilson *et al.,* 1993), and so diel vertical migration can impact access to prey species (Garthe *et al.,* 2007, 2000). Moreover, male gannets from Grassholm (Cox *et al.,* 2016), and elsewhere (Cleasby *et al.,* 2015; Lewis *et al.* 2002), perform overall shallower v-shaped dives than females (by ~1m, when accounting for body size differences; Cleasby *et al.,* 2015). This could relate to lower visibility in the early morning and late

evening, which may restrict access to deeper depths. Males from Bass Rock performed more U-shaped 'pursuit' dives than females, with no sex difference in the depth of U-shaped dives, but U-shaped dives were less likely at dusk and dawn (Cleasby *et al.,* 2015), which may also relate to visibility constraints. Although there was no observed sex difference in the selection for areas of high fishing vessel density, foraging in low light could increase the tendency of males to scavenge from fisheries, as artificial lighting may help them locate sparsely-distributed vessels (Arcos & Oro, 2002).

2.5.5 Isotopic segregation

Males had higher $\delta^{13}C$ and $\delta^{15}N$ values than females across all years, although there was some interannual variation in the strength of the effect (Figure 2.6). For example, a significant difference in $\delta^{13}C$ and $\delta^{15}N$ would not have been detected in 2010, likely due to the small sample of 8 females and 14 males (Table S2.7). Isotopic segregation occurred despite much broad-scale spatial overlap (Figure 2.2) indicating that the higher $\delta^{13}C$ and $\delta^{15}N$ values for males were unlikely to be due to differences in isotopic baselines (Kelly, 2000), such as the tendency for coastal areas to have lower $\delta^{13}C$ and $\delta^{15}N$ values than offshore waters (Cherel & Hobson, 2007; Hobson *et al.,* 1994). Our results may instead reflect sex differences in fine-scale habitat usage (Figure 2.4), diel segregation (males may have more access to deeper water species that migrate to shallower waters during dawn/dusk; Figure 2.5), or prey selection. While there were no sex differences in selection for fishing activity density (Figure 2.4), this may be due to temporal mismatch with the vessel data, and so scavenging may still explain isotopic differences. Firstly, higher $\delta^{13}C$ and $\delta^{15}N$ are consistent with a higher proportion of fisheries waste (Votier *et al.,* 2010), and previous gannet-borne camera studies and stable isotope mixing models suggest that male gannets may consume more discards (Stauss *et al.,* 2012; Votier *et al.,* 2013). However, Bodey *et al.* (2014) and Patrick *et al.* (2015) found no sex differences were found in spatial association with fishing vessels. Differences in the results of these studies could reflect the methods used or variation in sexual segregation between years and colonies.

Males and females may select different prey due to distinct nutritional requirements, possibly influenced by nutrient processing or parental roles (Morehouse *et al.,* 2010). Male Australasian gannets *Morus serrator* feed on fish

with a higher protein-to-lipid and water-to-lipid ratio and a higher trophic level than females (Machovsky-Capuska *et al.,* 2016). Nutritional requirements can be linked to dimorphism, but our results showed that the trophic niche was not driven by mass (Figure 2.6). Moreover, sex differences are unlikely to be due to female investment in the egg since the single egg clutch laid by the gannet is one of the smallest compared to female mass at 3.3% (Perrins, 1970; Western & Ssemakula, 1982), with a very low energy and lipid content (Ricklefs & Montevecchi, 1979). While sex-specific foraging may provide nutritionally different diets in gannets, there is no clear mechanism for this to be driven by distinct nutritional requirements.

2.6 Conclusion

Male and female gannets exhibited a number of differences in their foraging and isotopic niche, and long-term study revealed that these vary across years. On average, the strongest and most consistent difference was in isotopic niche segregation, which likely reflects differences in diet. Our results are consistent with competitive exclusion as a mechanism underlying these observed differences as females travel further to forage than males in some years but not others. Our results are also consistent with niche specialisation as a mechanism because we found consistent sex differences in trophic niche, even in years of spatial overlap. As such, our findings support the conclusion that competitive exclusion and specialisation are not mutually exclusive (Catry *et al.,* 2005). Since sex differences were largely consistent in terms of their direction, it appears that these factors are also influenced by differing responses to environmental conditions that are not yet fully understood. As many aspects of sexual segregation vary interannually, our results show that analyses based on single years may reflect general patterns. We emphasise the value of long-term studies for demonstrating dynamic niche segregation and highlight the importance of determining the environmental factors that drive such variation.

2.7 Supplementary material

Table S2.1 provides measurements and statistics comparing biometrics for males and females. Table S2.2 gives the values and sample sizes for foraging trip range and duration plotted in Figure 2.1 along with home ranges. Table S2.3 provides model estimates for trip range and duration. Table S2.4 provides estimates for spatial overlap equivalent to those in Figure 2.3 with 29 random subsamples to account for sample size variation. Table S2.5 provides estimates and measures of significance for habitat selection models plotted in Figure 2.4. Table S2.6 provides values for assessing the fit of habitat selection models plotted in Figure 2.4. Table S2.7 gives $\delta^{13}C$ and $\delta^{15}N$ stable isotope values and sample sizes for the data plotted in Figure 2.6. Table S2.8 provides model estimates for stable isotope values of $\delta^{13}C$ and $\delta^{15}N$.

Table S2.1. Biometric measurements for chick-rearing northern gannets *Morus bassanus* at Grassholm, UK, measured in 2006 and 2008–17. There were no sex differences in bill length or wing length, although females were 6.8% (193g) heavier than males.

	Female		Male		Linear Model			
	Mean ± SD	n	Mean ± SD	n	Adj. r^2	F	df	p
Bill length (mm)	98.3 ± 2.91	190	98.24 ± 2.90	210	-0.002	0.043	1, 398	0.835
Wing chord (cm)	49.3 ± 0.9	180	49.3 ± 0.8	203	-0.003	0.004	1, 381	0.948
Mass (g)	3032 ± 259	192	2839 ± 208	217	0.143	69.14	1, 407	<0.001

Table S2.2. Mean foraging trip metrics ± standard error derived from GPS loggers deployed on Grassholm, UK, for 634 foraging trips from 297 northern gannets *Morus bassanus*. Home range is derived from 95% utilisation distributions calculated using kernel density estimation.

	Female					Male				
Year	n trips	n birds	Foraging range (km)	Trip duration (hours)	Home range (km^2)	n trips	n birds	Foraging range (km)	Trip duration (hours)	Home range (km^2)
2006	12	10	189 ± 30	33.9 ± 5.3	46,786	17	13	78 ± 10	18.4 ± 3.7	21,011
2010	26	6	160 ± 17	26.9 ± 3.3	66,064	60	16	146 ± 14	22.9 ± 1.8	75,269
2011	88	20	116 ± 9	23.7 ± 2.7	65,298	115	25	104 ± 5	18.5 ± 1.4	52,993
2012	21	20	148 ± 14	27.4 ± 2.9	47,596	26	20	115 ± 11	20.9 ± 2.1	38,021
2013	45	27	134 ± 9	21.5 ± 1.7	36,529	31	20	115 ± 11	19.6 ± 2.2	36,300
2014	26	22	147 ± 13	20.2 ± 2.2	34,419	24	19	96 ± 8	15.4 ± 1.7	30,029
2015	10	7	101 ± 13	17.6 ± 21	18,664	31	20	93 ± 6	18.7 ± 1.7	26,130
2016	27	17	81 ± 11	18.9 ± 3.4	28,063	40	21	67 ± 6	16.0 ± 1.9	20,151
2017	17	11	139 ± 12	36.8 ± 4.4	41,594	18	10	136 ± 12	39 ± 6.3	40,878
All	272	138	129 ± 5	24.2 ± 1.2	88,883	362	159	107 ± 4	20.1 ± 0.8	68,800

Table S2.3. Linear Mixed Model estimates ± standard error for foraging trip duration and range for northern gannets *Morus bassanus* in relation to sex, year and mass (kg), with bird ID fitted as a random intercept. Estimates are from the model with the lowest AICc (see Table 2.1), given on the Box-Cox transformed scale.

	Duration (h)	SE	Range (km)	SE
Intercept – 2006, female	3.021	0.285	6.314	0.783
Sex – male	-0.150	0.039	-1.892	0.931
Year – 2010	-0.023	0.120	0.313	0.235
Year – 2011	-0.134	0.117	-0.022	0.231
Year – 2012	-0.021	0.127	0.175	0.248
Year – 2013	-0.102	0.123	0.131	0.241
Year – 2014	-0.172	0.131	0.168	0.258
Year – 2015	-0.147	0.128	-0.090	0.252
Year – 2016	-0.261	0.121	-0.536	0.238
Year – 2017	0.175	0.130	0.223	0.255
Mass (kg)	-0.272	0.081	-0.756	0.236
Sex:Mass	-	-	0.533	0.312

Table S2.4. Estimated overlap (Bhattacharyya's affinity, BA) in male and female northern gannet *Morus bassanus* utilisation distributions (UD) randomly subsampled to the sample size of 2006 (29 trips). P is the proportion of simulation BAs that did not exceed the observed BA. The mean BA was slightly lower for random samples of 29 trips for 2010–17 (0.678 compared to 0.794), but the segregation was not significantly different from the null distribution.

Year	Random sample no.	100% UD	
		BA	P
2010	1	0.598	0.934
	2	0.598	0.653
	3	0.528	0.186
2011	1	0.639	0.558
	2	0.729	0.785
	3	0.545	0.405
2012	1	0.745	0.414
	2	0.677	0.610
	3	0.746	0.802
2013	1	0.603	0.135
	2	0.624	0.070
	3	0.711	0.345
2014	1	0.660	0.053
	2	0.719	0.150
	3	0.642	0.151
2015	1	0.704	0.209
	2	0.808	0.710
	3	0.770	0.782
2016	1	0.863	0.723
	2	0.716	0.635
	3	0.740	0.397
2017	1	0.579	0.084
	2	0.691	0.558
	3	0.603	0.077

Table S2.5. Outputs from habitat selection models for male and female northern gannets *Morus bassanus* for the sex:habitat interaction from a binomial GAM fitted with a residual autocovariate smoother to account for spatial autocorrelation (*p<0.05, **p<0.01, ***p<0.001). This models the probability of locations being classed as a foraging location rather than a pseudo-absence in response to four habitat variables: sea surface temperature (°C), chlorophyll-a concentration, thermal fronts (composite of strength, proximity and persistence) and fishing activity (number of Vessel Monitoring System records travelling at fishing speed).

Year	Sex interaction	Habitat variable			
		Sea surface temperature	Chlorophyll-a concentration	Thermal fronts	Fishing density
all	Estimate	**-0.349**	**0.601**	**0.113**	0.055
	p value	**<0.001*** **	**<0.001*** **	**0.006** **	0.295
	Δ AIC	**-34.05**	**-78.64**	**-5.39**	0.90
2006	Estimate	**-2.558**	**1.967**	**0.744**	-0.159
	p value	**<0.001*** **	**<0.001*** **	**0.001** **	0.755
	Δ AIC	**-31.23**	**-17.70**	**-8.57**	1.90
2010	Estimate	**-0.381**	**-0.539**	0.062	-0.114
	p value	**0.001** **	**0.001** **	0.425	0.180
	Δ AIC	**-8.56**	**-9.07**	1.37	0.24
2011	Estimate	**-0.501**	NA	0.002	0.150
	p value	**<0.001*** **	NA	0.980	0.109
	Δ AIC	**-11.03**	NA	2.00	-0.64
2012	Estimate	**-0.899**	-0.251	0.535	-0.037
	p value	**0.045***	0.527	0.055.	0.877
	Δ AIC	**-2.15**	1.59	-1.39	1.98
2013	Estimate	**-0.671**	0.651	0.017	0.272
	p value	**0.011***	0.177	0.851	0.112
	Δ AIC	**-4.65**	0.18	1.97	-0.89
2014	Estimate	-0.019	0.152	**0.794**	-0.140
	p value	0.970	0.842	**<0.001*** **	0.645
	Δ AIC	2.00	1.96	**-16.38**	1.79
2015	Estimate	**-0.868**	0.230	-0.091	0.175
	p value	**0.029***	0.735	0.672	0.664
	Δ AIC	**-2.41**	1.89	1.82	1.80
2016	Estimate	0.156	0.643	-0.105	-0.344
	p value	0.600	0.282	0.640	0.412
	Δ AIC	1.73	0.86	1.78	1.27

Table S6. Assessment of habitat selection models containing a habitat variable, sex and sex:habitat interaction (Table S2.5). Kappa and AUC (area under the Receiver Operating Characteristic curve) are derived from a confusion matrix based on the original data. Kappa is the proportion of correct predictions in relation to random chance (max. 1). AUC ranges from 0 to 1, where 0.5 is random, and higher values indicate better model performance. The Boyce index for assessing resource selection functions is suitable for presence-only models. It ranges from -1 to 1, where 0 indicates random and positive values show that the prediction is consistent with the presence data distribution.

Year	Measure	Habitat variable			
		Sea surface temperature	Chlorophyll-a concentration	Thermal fronts	Fishing density
all	Kappa	NA	NA	NA	NA
	AUC (ROC)	0.991	0.990	0.991	0.991
	Boyce index	0.853	0.909	0.891	0.827
2006	Kappa	0.948	0.949	0.950	0.950
	AUC (ROC)	0.997	0.996	0.996	0.997
	Boyce index	0.746	0.779	0.701	0.826
2010	Kappa	0.852	0.853	0.848	0.846
	AUC (ROC)	0.981	0.981	0.981	0.981
	Boyce index	0.844	0.873	0.879	0.834
2011	Kappa	0.880	0.885	0.880	0.882
	AUC (ROC)	0.987	0.985	0.986	0.987
	Boyce index	0.891	0.926	0.850	0.822
2012	Kappa	0.950	0.947	0.947	0.948
	AUC (ROC)	0.996	0.996	0.996	0.996
	Boyce index	0.769	0.809	0.684	0.697
2013	Kappa	0.935	0.934	0.934	0.934
	AUC (ROC)	0.995	0.995	0.995	0.995
	Boyce index	0.779	0.795	0.737	0.596
2014	Kappa	0.953	0.953	0.955	0.954
	AUC (ROC)	0.997	0.997	0.997	0.997
	Boyce index	0.771	0.715	0.783	0.820
2015	Kappa	0.943	0943	0.943	0.943
	AUC (ROC)	0.995	0.995	0.996	0.995
	Boyce index	0.766	0.655	0.767	0.596
2016	Kappa	NA	0.944	0.944	0.946
	AUC (ROC)	0.991	0.994	0.995	0.995
	Boyce index	0.853	0.915	0.849	0.872

Table S2.7. Mean stable isotope values (per mil) ± standard error from northern gannet *Morus bassanus* red blood cells collected for 361 individuals on Grassholm during nine breeding seasons.

Year	Female			Male		
	n	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
2006	16	-17.84 ± 0.06	14.62 ± 0.09	20	-16.98 ± 0.14	15.54 ± 0.14
2008	22	-18.03 ± 0.05	13.69 ± 0.08	18	-17.68 ± 0.06	14.25 ± 0.12
2009	10	-17.99 ± 0.07	14.78 ± 0.10	17	-17.59 ± 0.09	15.40 ± 0.13
2010	8	-17.88 ± 0.17	14.18 ± 0.19	14	-17.43 ± 0.13	14.51 ± 0.23
2011	21	-17.76 ± 0.10	14.53 ± 0.13	30	-17.18 ± 0.08	15.12 ± 0.10
2012	24	-17.64 ± 0.09	15.14 ± 0.12	30	-17.25 ± 0.10	15.63 ± 0.10
2013	27	-17.78 ± 0.10	14.36 ± 0.14	24	-17.59 ± 0.12	15.17 ± 0.14
2014	15	-17.47 ± 0.11	13.84 ± 0.14	11	-16.93 ± 0.10	14.49 ± 0.14
2016	25	-17.63 ± 0.10	14.46 ± 0.14	29	-16.92 ± 0.09	15.08 ± 0.09
All	168	-17.77 ± 0.03	14.41 ± 0.05	193	-17.28 ± 0.04	15.16 ± 0.05

Table S2.8. Linear Model estimates ± standard error for stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ from northern gannet *Morus bassanus* red blood cells in relation to sex, year and mass. Estimates are from the model with the lowest AICc (see Table 2.3).

	$\delta^{13}C$	SE	$\delta^{15}N$	SE
Intercept – 2006, female	-19.44	0.479	13.352	0.565
Sex – male	2.316	0.695	1.858	0.780
Year – 2008	-0.061	0.152	-1.052	0.134
Year – 2009	-0.070	0.182	0.005	0.146
Year – 2010	0.022	0.194	-0.765	0.152
Year – 2011	0.111	0.154	-0.241	0.127
Year – 2012	0.296	0.152	0.331	0.133
Year – 2013	0.156	0.146	-0.280	0.126
Year – 2014	0.494	0.164	-0.872	0.147
Year – 2016	0.293	0.145	-0.288	0.122
Mass (g)	0.0005	0.0001	0.0004	0.0002
Sex:Mass	-0.0005	0.0002	-0.0004	0.0003
Sex:Year – 2008	-0.631	0.214	-	-
Sex:Year – 2009	-0.568	0.236	-	-
Sex:Year – 2010	-0.474	0.249	-	-
Sex:Year – 2011	-0.278	0.205	-	-
Sex:Year – 2012	-0.433	0.212	-	-
Sex:Year – 2013	-0.769	0.201	-	-
Sex:Year – 2014	-0.430	0.236	-	-
Sex:Year – 2016	-0.223	0.195	-	-

Chapter 3 – Energetic costs of foraging in a wide-ranging marine predator

3.1 Abstract

The cost of foraging forms a large part of the energy budget of many species and is particularly important for those provisioning offspring. As seabirds breed on land but generally forage at sea, their food sources can be distant from their nests. Intra-population differences in foraging range lead to substantial individual variation in foraging effort and behaviour. Foraging effort, measured by foraging trip duration and distance travelled, is often used as a proxy for food availability or competitive pressure. However, flight costs also vary with factors such as wing loading and wind conditions, so it is important to assess the effectiveness of these metrics of effort. Breeding northern gannets *Morus bassanus* are central-place foragers that travel hundreds of kilometres in a single trip but have a costly mode of flight. Here we investigate the relative importance of different behaviours during a foraging trip, using simultaneous GPS logger and accelerometer deployments (to measure foraging effort) along with either barometric pressure altimeters (to estimate flight height) or video cameras (to record behaviour). We used video-validated acceleration to label flapping flight, passive flight (gliding/soaring), plunge dive, takeoff and resting on the water to two-second intervals. We calculated overall dynamic body acceleration (ODBA) as a proxy for energetic expenditure (n = 26). Flapping flight contributed most to the energetic expenditure of foraging trips, takeoff was the costliest behaviour per unit time, and resting on the water made up most of the time spent on foraging trips. Variation in mean ODBA was driven by time spent performing behaviours rather than variation in the costs of individual behaviours. Despite this, there is variation in the energetic expenditure required to gain altitude. Furthermore, there was little individual variation in the proportions of time spent performing each behaviour. Finally, we find that trip duration, distance travelled and mean speed derived from GPS loggers are good metrics of foraging effort. Overall, we identify the drivers of foraging effort for gannets, and highlight the benefits of using multiple bio-logging techniques to study foraging behaviour.

Keywords: dynamic body acceleration; flight height; altitude; GPS; northern gannet; *Morus bassanus*; seabird

3.2 Introduction

The energetic cost of locomotion is key to understanding the movement decisions made by animals (Shepard *et al.,* 2013; Wilson *et al.,* 2006). In particular, the cost of foraging forms a large part of the time and energy budgets of most wild animals (Emlen, 1966), particularly when resources are patchily distributed (Macarthur & Pianka, 1966). A variety of modes of travel have evolved; flight is the fastest, allowing for the longest animal journeys on earth (Egevang *et al.,* 2010), but it has the highest energetic cost per unit time (Guigueno *et al.,* 2019). As such, it is crucial to minimise flight costs. For example, soaring can be employed to gain lift from the environment by taking advantage of rising air from thermals (Shepard *et al.,* 2011), shear winds, convergences, and updrafts from ridges or waves (Richardson, 2011; Weimerskirch *et al.,* 2000). These tactics allow for long-distance flight at very low mechanical cost (Sachs *et al.,* 2012). However, many species use continuous wingbeats to remain airborne (Bishop *et al.,* 2015), with the remaining using a mixture of flapping flight, gliding and soaring (Vincze *et al.,* 2019).

The balance between the cost of travel and the food gained is particularly important for central-place foragers rearing young away from their food source (Kacelnik, 1984). For example, colonial seabirds breed on land but forage at sea, and their food sources tend to be distant from their nests (Rolland *et al.,* 1998). Colonial breeders often travel further due to competition with other members of the colony (Ashmole, 1963; Jovani *et al.,* 2016; Lewis *et al.,* 2001; Oppel *et al.,* 2015), and low food availability (Hamer *et al.,* 2007; Davies *et al.,* 2013; Paiva *et al.,* 2013; Thorne *et al.,* 2015; Warwick-Evans *et al.,* 2016a). As such, differences in the energetic costs of foraging trips can be substantial, but we know little about whether individuals adjust their tactics for foraging trips of different lengths.

Measures of foraging effort are particularly useful for understanding seabird biology, as they integrate the effects of local environmental conditions, prey availability and competitive pressure (Davies *et al.,* 2013; Hamer *et al.,* 2007; Lewis *et al.,* 2006; Paiva *et al.,* 2013). However, measures of effort tend to rely on distance travelled or time spent away from the nest (Lewis *et al.,* 2001). Many seabirds spend much of their time away from the colony resting on the water, and the time spent resting can have a substantial impact on energy and time budgets (Jodice *et al.,* 2003). Therefore, we might expect a greater proportion of resting

on overnight trips, which would reduce the correlation between energy expenditure and trip duration.

Flight is a key energetic component of long-distance foraging trips, but energy-saving gliding and soaring, are less well studied in species with mixed flight styles. Given that flight costs vary with factors such as wing loading (Suryan *et al.,* 2008), wing morphology (Vincze *et al.,* 2019) and wind conditions (Elliott *et al.,* 2014; Weimerskirch *et al.,* 2012), it is important to assess the effectiveness of trip duration and distance travelled as metrics of effort. Flight costs may also relate to the current behavioural state of the individual. For example, commuting to a foraging site involves straight, fast, efficient flight, while searching for prey involves more costly, tortuous flight (Andersson, 1981; Fauchald & Tveraa, 2003). Altitude gained can also improve prey detection (Andersson *et al.,* 2009). As foraging is more energetically expensive than commuting flight, longer trips may be less energetically expensive per unit time. However, seabirds are limited in their capacity to carry food so longer trips providing the same total delivery to the chick will be less profitable overall.

Gannets (three species in the genus *Morus*) travel hundreds of kilometres to acquire a meal for themselves or their offspring (Besel *et al.,* 2018; Botha *et al.,* 2017: Hamer *et al.,* 2007). Despite this, northern gannets *M. bassanus* have a high cost of foraging as indicated by a field metabolic rate of 4865 kJ/d, which is 6.6 times the basal metabolic rate (Birt-Friesen *et al.,* 1989). The Australasian gannet *M. serrator* has a field metabolic rate double during flight compared to resting (Green *et al.,* 2009), and northern gannet energy expenditure estimated from accelerometry is much higher during area restricted search than during commuting flight (Amélineau *et al.,* 2014). Flapping has been directly linked to energy use in Cape gannets *M. capensis,* for which accelerometers and electrocardiogram recorders showed almost instantaneous heart rate change when switching between gliding and flapping flight, at 217.2 and 255.5 bpm respectively (Ropert-Coudert *et al.,* 2006). Wind strength and direction have a large impact on northern gannet energy expenditure, but they do not optimise their flight alignment to wind direction, likely due to prey patch location (Amélineau *et al.,* 2014) and individual foraging site fidelity (Patrick *et al.,* 2015; Votier *et al.,* 2017; Wakefield *et al.,* 2015). As such, the energy saved by gliding or soaring during the commuting part of their flight may play a key role during these long-distance trips.

To investigate northern gannet (hereafter “gannet”) foraging effort, we use time-matched bird-borne video cameras and accelerometers to classify the following behaviours to two-second intervals across entire foraging trips: takeoff, flapping flight, passive flight, plunge dive, underwater, landing on water, active on water, and resting on water. Dynamic body movement calculated from tri-axial acceleration is a good proxy for energy use as shown by measurements of heart rate (Halsey *et al.,* 2008) and oxygen consumption (Wilson *et al.,* 2006). Using overall dynamic body acceleration (ODBA) as a proxy for energetic expenditure, we compare the relative importance of these behaviours in terms of ODBA and duration. Using time-matched accelerometers and barometric altimeters, we investigate the relationship between flight ODBA and the loss or gain of altitude. We then use simultaneous deployments of GPS loggers to compare metrics of foraging effort derived from accelerometry with metrics derived from GPS (trip duration, foraging range, total distance travelled, mean speed, and the percentage of time spent resting/searching/travelling). We included foraging range, as well as total distance travelled, as it is less affected by the sampling frequency, making it more comparable across studies.

3.3 Methods

3.3.1 Study site and sampling

Sampling was conducted on Grassholm Island, UK (51º43’N, 05º28’W), an offshore gannet colony of approximately 36,000 breeding pairs (Murray *et al.,* 2015b). Sampling took place in 2016 and 2017 during chick-rearing (mid-July to mid-August). We caught gannets with a pole and crook during the changeover between parents at the nest, so that the chick was not unattended and that foraging trips began immediately after release. We equipped a subset of individuals with a GPS logger (Mobile Action Technology i-gotU 120, 18g), a tri-axial accelerometer (Gulf Coast Data Concepts X16-mini, 16g), and a video camera (Perthold Engineering BirdCam, 24g). We equipped the remaining individuals with a GPS logger, an accelerometer, and an altimeter (MSR-145W air pressure and temperature recorder, 18g). We attached GPS loggers, cameras and altimeters to the central tail feathers with Tesa® 4651 tape. We placed cameras on top of the tail facing towards the head at a slightly elevated angle (Figure S3.1). We placed altimeters on the underside of the tail with the sensor facing downwards. We taped accelerometers to the lower back feathers (Figure

S3.1), to more accurately reflect body movement, and reduce the impact on flight by spreading logger weight toward the centre of gravity (Vandenabeele *et al.,* 2014). The combined logger weight of 58g was 2.0% of the mean weight of tagged birds (2850g) and 2.4% of the lightest (2450g). Cameras were programmed to film for 30 mins and then standby for 30 mins until the battery was exhausted. This led to an average of 3.9 hours of footage per deployment, across the first nine hours of each foraging trip. GPS loggers recorded a fix every minute, altimeters recorded air pressure and temperature at 1hz, and accelerometers recorded at 50hz. We recaptured birds after at least one foraging trip and recovered the loggers. Previous studies have shown no effects of loggers weighing 20g, 30g or 70g on the foraging trip duration or body mass of chick-rearing gannets (Hamer *et al.,* 2009, 2007; Lewis *et al.,* 2002). We fitted all individuals with a metal ring and a colour ring with an alpha-numeric code for re-sighting and marked them with non-toxic animal dye (All-weather paintstik®) to aid recapture. We measured wing length (maximum flattened chord to the nearest 1cm), bill-to-feathering and tarsus length (to the nearest 0.1mm), and weight (to the nearest 50g). We took a 1–2ml blood sample from the tarsal vein using 23–25-gauge needles for molecular sexing. Protocols were completed under licence from Natural Resources Wales (22478:OTH:SB:2010), the British Trust for Ornithology (A4257) and the UK Home Office (30/3065). Adult gannets are highly repeatable in their foraging locations, so one trip per individual is likely to be representative (Patrick *et al.,* 2015; Votier *et al.,* 2017; Wakefield *et al.,* 2015).

3.3.2 GPS data

We extracted the first complete foraging trip for each bird using the point at which the birds left a radius of 200m from the centre of the colony. We recorded trip duration and calculated the foraging range (maximum distances from the colony), and the total distance travelled using the 'geosphere' R package (Hijmans, 2017). To calculate mean speed, we divided total distance travelled by trip duration. We classified behaviours from the GPS data into 'rest', 'foraging' and 'travel' based on speed, acceleration and tortuosity thresholds (see Wakefield *et al.,* 2013; Bennison *et al.,* 2017).

3.3.3 Energetic expenditure from acceleration

As a proxy for energy expenditure, we calculated overall dynamic body acceleration (ODBA) (Halsey *et al.,* 2011, 2008; Wilson *et al.,* 2006). The relationship between dynamic body acceleration and energetic expenditure has been validated with Vectorial Dynamic Body Acceleration (VeDBA; which is highly correlated with ODBA) using doubly-labelled water for the closely-related Australasian gannet *Morus serrator* with an $r^2 = 0.63$ (Angel, 2015). To estimate static acceleration, we calculated a running mean for each axis (surge, heave and sway) across a one-second period (Collins *et al.,* 2015). To produce dynamic acceleration, we calculated the absolute difference between raw and static acceleration. The sum of the dynamic acceleration across the three axes is the ODBA (Qasem *et al.,* 2012).

3.3.4 Behavioural classification from acceleration

We used video-validated accelerometry to classify behavioural states at two-second intervals across the foraging trip (Shepard *et al.,* 2008). First, we time-matched the videos and acceleration data to the GPS data and extracted the first complete foraging trip. We rotated the acceleration data for each individual to account for differences in tag placement using the 'tagtools' R package (DeRuiter, 2019). Then we first generated a training dataset using the time-matched video footage, coding the following behaviours: 'flight', 'plunge dive', 'underwater' and 'rest on water', partly using BORIS video coding software (Friard & Gamba, 2016). For ten birds, we labelled a subset of acceleration data in Framework4 (Walker *et al.,* 2015) with the following eight behaviours: 'flapping flight', 'passive flight', 'plunge dive', 'underwater', 'land on water' (transition between flight and water with no dive), 'rest on water', 'preen' and 'takeoff' (transition between water and flight). We extracted the first two seconds (100 records at 50hz) of each labelled section to form a training dataset (Collins *et al.,* 2015). We calculated 28 metrics for each section: mean ODBA and VeDBA (the square root of the sum of the square of each axis of dynamic acceleration); minimum, maximum, mean and standard deviation of surge, heave, sway, pitch and roll; and cumulative positive and negative values for surge, heave and sway.

We used a random forest model to characterise the training dataset and predict behavioural states for the full dataset using the 'randomForest' R package (Liaw & Wiener, 2002). We used 10,000 trees per model. For each node within a

tree, we randomly sampled five metrics ('mtry' = 5, the square-root of the number of variables). We then divided the full foraging trip into two-second sections and used the model to predict the behaviour for each section. The out of bag error rate was 0.7%, and 44.2% of the errors were not important as behaviours were interchangeable, such as passive and flapping flight (Table 3.1, Table 3.2). See Figure S3.2 for the relative contributions of each metric to the accuracy of the model.

Table 3.1. Confusion matrix for the random forest model for classification of northern gannet *Morus bassanus* behaviours from acceleration data (out of bag error rate = 0.7%). Colours show error type and importance (Green = correct, grey = incorrect but not important as behaviours are interchangeable, yellow = incorrect but important as behaviours are not interchangeable, red = incorrect and most important as plunge-diving is the main indicator of foraging).

Behaviour	Dive	Flap	Land	Passive	Preen	Takeoff	Under	Water
Plunge dive	**188**	0	0	0	0	0	0	0
Flapping	0	**15118**	0	4	5	1	0	1
Land (water)	9	14	**5**	5	12	4	1	1
Passive flight	0	5	0	**15231**	7	0	0	1
Preen (water)	3	12	0	6	**1306**	28	0	37
Takeoff	0	0	0	0	2	**1327**	0	0
Underwater	0	3	0	1	20	1	**15**	2
Rest (water)	1	1	0	19	17	1	0	**2078**

Table 3.2. Summary of classifications by error type from Table 3.1.

Classification	Count	Percentage
Total	35,492	100 %
Correct	35,268	99.4 %
Incorrect, not important	99	0.28 %
Incorrect, important	112	0.32 %
Incorrect, most important	13	0.04 %

We then used logic-based corrections to reassign labels that were incorrect from context (Table S4.1). We increased the training dataset for periods when video footage was not available by comparing traces to the video-validated training dataset (this could not be done for 'dive', 'land' or 'underwater' as these could not be identified from acceleration alone). To assess the model, we used it to predict behaviour and then visually assessed the predictions. We then increased the amount of labelled training data for periods where predictions were poor. Dives are a key behaviour, but we have a limited sample size, so we duplicated the training dataset for dives to increase their sample relative to other behaviours. For each individual, we calculated the time spent performing each behaviour and the mean ODBA for each behaviour. We visually reassessed the final model, which had a mean error rate of 1.6% across 26 individuals, ranging from 0.003% to 7.97% (Table S3.2). We then corrected the activity budgets according to the visual assessment, where possible. Underwater wingbeats and landing on the water were rare and not easily detected, so they were combined with 'preen' to form 'water active' for activity budgets and mean ODBA per behaviour. Total ODBA was calculated as the mean ODBA multiplied by the duration in hours.

3.3.5 Altitude data processing

Pressure loggers were programmed to record at 1Hz. The barometric formula was used to estimate flight height above sea level *z* in meters from the pressure data (Berberan-Santos *et al.,* 1997):

$$z = -\frac{kT}{mg}\ln\left(\frac{P}{P_0}\right)$$

where *P* and P_0 are the atmospheric pressures (Pascals) at height *z* (m) and at sea level respectively; *k* is the universal gas constant for air (8.31432 N m/(mol K)); *m* is the molar mass of air (0.0289644 kg/mol); *g* is the acceleration due to gravity (m/s); and *T* is the temperature of the atmospheric layer between z_0 and *z*. We used the known height of the colony as the starting pressure and further calibrated the pressure at sea level when the birds take off after a period on the water (see Cleasby *et al.,* 2015a). We limited P_0 to be the within the range recorded on pressure maps of the colony's foraging range available at 6-, 12- or 18-hour intervals (Met Office, metoffice.gov.uk). Flight altitude measured at 1hz was then smoothed over an 11-second window (Cleasby *et al.,* 2015a). We

extracted 7,982 30-second segments of continuous flight using the behavioural classifications from acceleration and calculated the change in altitude and the cumulative altitude gain over 30 seconds. We excluded 8 segments with a climb rate above 2.5ms^{-1} or a descent rate above 5ms^{-1}, as these are likely to be erroneous (Hedenström *et al.,* 2002).

3.3.6 Statistical analysis

We tested the correlations between the mean ODBA of the foraging trip and the mean ODBA for each individual behaviour, and the percentage of time during the foraging trip assigned to each behaviour. We then tested the correlations between three metrics of effort derived from acceleration data (mean trip ODBA, hours spent flying and hours spent resting), and four metrics derived from GPS data (trip duration, range, total distance travelled and mean speed). We analysed altitude change over 30-second periods in relation to mean ODBA using a Linear Mixed Model with bird ID fitted as a random slope and intercept.

3.4 Results

3.4.1 Behavioural classification

We classified behaviours during one complete foraging trip for 26 individuals at two-second intervals (e.g. Figure 3.1). Visual assessment showed that the method correctly classified 98.5% of the 1,402,250 records (21,083 errors, such as those shown in Figure S3.3).

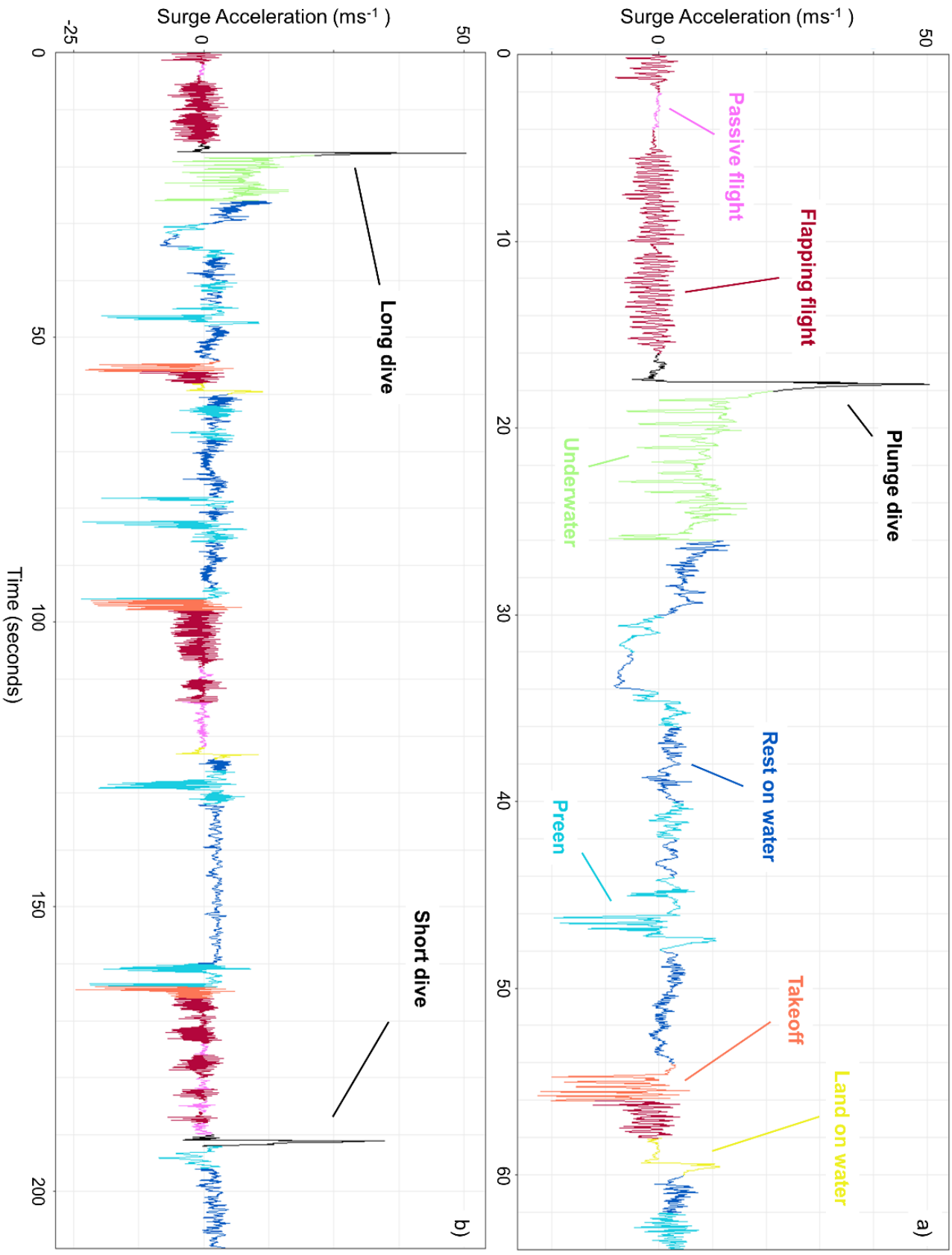


Figure 3.1. Behavioural classification of northern gannet *Morus bassanus* foraging at two-second intervals using a video-validated random forest model with logic correction. Behaviours are shown in the surge axis over a) a 64-second period, and b) a 210-second period with the same start time to show a long dive with underwater wingbeats in comparison to a short dive without underwater wingbeats.

3.4.2 Relative ODBA and activity budgets

Behaviours varied in mean ODBA (Table 3.3, Figure 3.2), with flapping flight having the highest total ODBA, followed by rest on water. Takeoff had the highest ODBA per unit time (Table 3.3, Figure 3.2). There was also variation in the time spent performing each behaviour (Table 3.3, Figure 3.3), with the majority of the time spent resting (67.48%), followed by flapping flight (20.46%), passive flight (8.70%), active on the water (2.42%), unknown flight (0.55%), takeoff (0.28%) and aerial plunge dive (0.10%). There were no sex differences in total ODBA (estimate = 2.647 ± 3.486, $\chi^2_{1,24} = 0.574$, p = 0.449) or mean ODBA (estimate = -0.004 ± 0.026, $F_{1,24} = 0.024$, p = 0.878). Females had a higher mean ODBA for takeoff (estimate = -0.257 ± 0.102, $F_{1,24} = 6.357$, p = 0.019), with no other sex differences in individual behaviours (Table S3.3, Figure S3.4).

Table 3.3. Means ± standard errors across 26 northern gannets *Morus bassanus* foraging trips for the relative contributions of each behaviour to the energetic and activity budgets, where total Overall Dynamic Body Acceleration (ODBA) is the mean ODBA multiplied by the time in hours.

Behaviour	Total ODBA	Mean ODBA	Time per trip	Trip percentage
Flapping flight	5.56 ± 0.72	0.98 ± 0.01	5.50 ± 0.69 hr	20.46 ± 1.46 %
Water rest	4.62 ± 0.88	0.21 ± 0.004	20.98 ± 3.48 hr	67.48 ± 2.15 %
Water active	0.66 ± 0.18	0.79 ± 0.01	49.71 ± 12.70 min	2.42 ± 0.24 %
Passive flight	0.63 ± 0.09	0.27 ± 0.01	2.30 ± 0.31 hr	8.70 ± 0.90 %
Takeoff	0.18 ± 0.03	2.36 ± 0.06	4.61 ± 0.63 min	0.28 ± 0.02 %
Plunge dive	0.07 ± 0.02	1.78 ± 0.05	1.60 ± 0.24 min	0.10 ± 0.01 %
Unknown flight	0.07 ± 0.02	0.50 ± 0.03	15.64 ± 10.83 min	0.55 ± 0.22 %

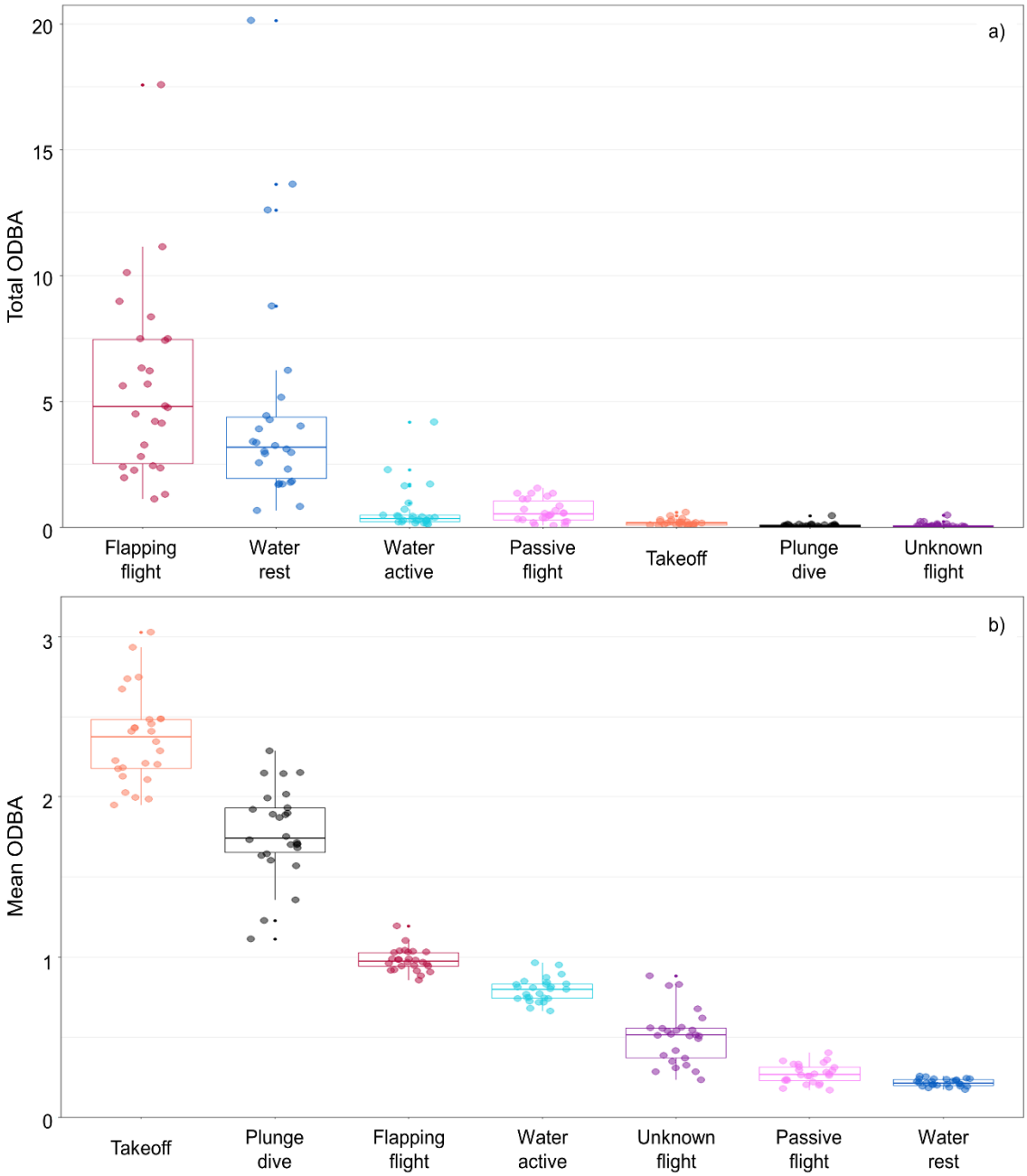


Figure 3.2. The a) total and b) mean Overall Dynamic Body Acceleration (ODBA) for each behaviour performed by northern gannets *Morus bassanus* with each jittered circle showing the mean for an individual across one foraging trip. The total ODBA is the mean ODBA for each behaviour multiplied by the hours spent performing it.

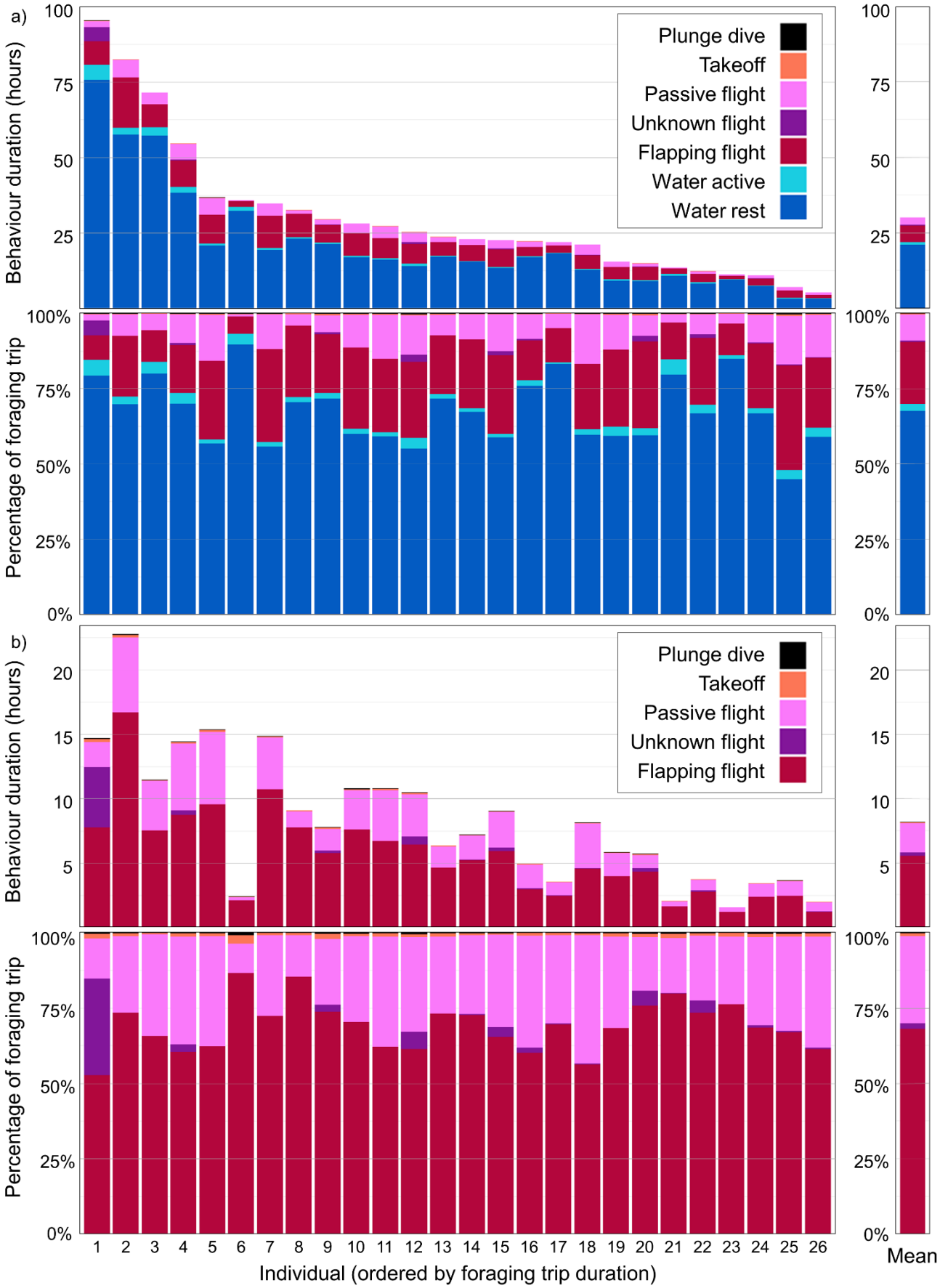


Figure 3.3. Activity budgets for 26 northern gannet *Morus bassanus* foraging trips, and a mean activity budget across all individuals, for a) all behaviours and b) only flight behaviours. Each bar represents a single trip made by a different individual.

3.4.3 Metrics of foraging effort from acceleration

The mean ODBA for the foraging trip did not strongly correlate with the mean ODBA of any particular behaviour (Figure 3.4a), with the strongest correlation being between mean ODBA and the ODBA of resting on the water ($r = 0.46$, $p = 0.02$). Mean ODBA for the foraging trip was strongly negatively correlated with the percentage of time spent resting, and positively correlated with the time spent in flight, takeoff and plunge dive, but not correlated with time spent in being active on the water, which is mainly preening (Figure 3.4b).

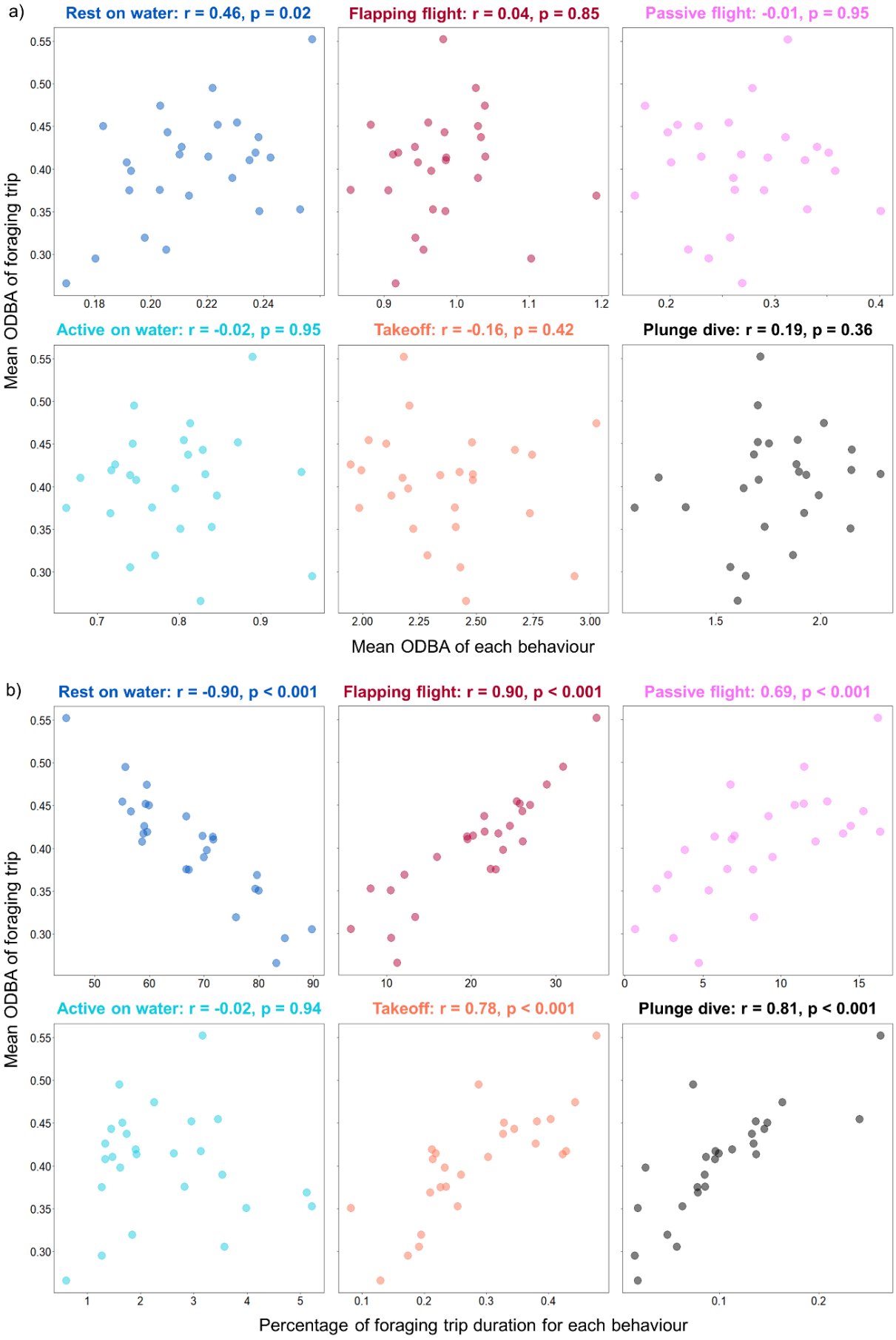


Figure 3.4. Correlations between mean ODBA for the entire foraging trip and a) the mean for each behaviour, or b) the percentage of time spent performing each behaviour.

3.4.4 Flight costs and altitude

We recorded time-matched GPS, acceleration and altitude data for eight individuals. Figure 3.5 shows an example of a foraging trip plotted by latitude longitude and altitude. We extracted 7,974 30-second periods of continuous flight. The change in altitude showed a positive relationship with mean ODBA over each 30-second segment (LMM: estimate ± SE = 6.212m ± 2.077, F_1 = 8.948, p = 0.017, Figure 3.6). There was a high level of variation (Figure 3.7), with more variation within than between individuals (Figure S3.5).

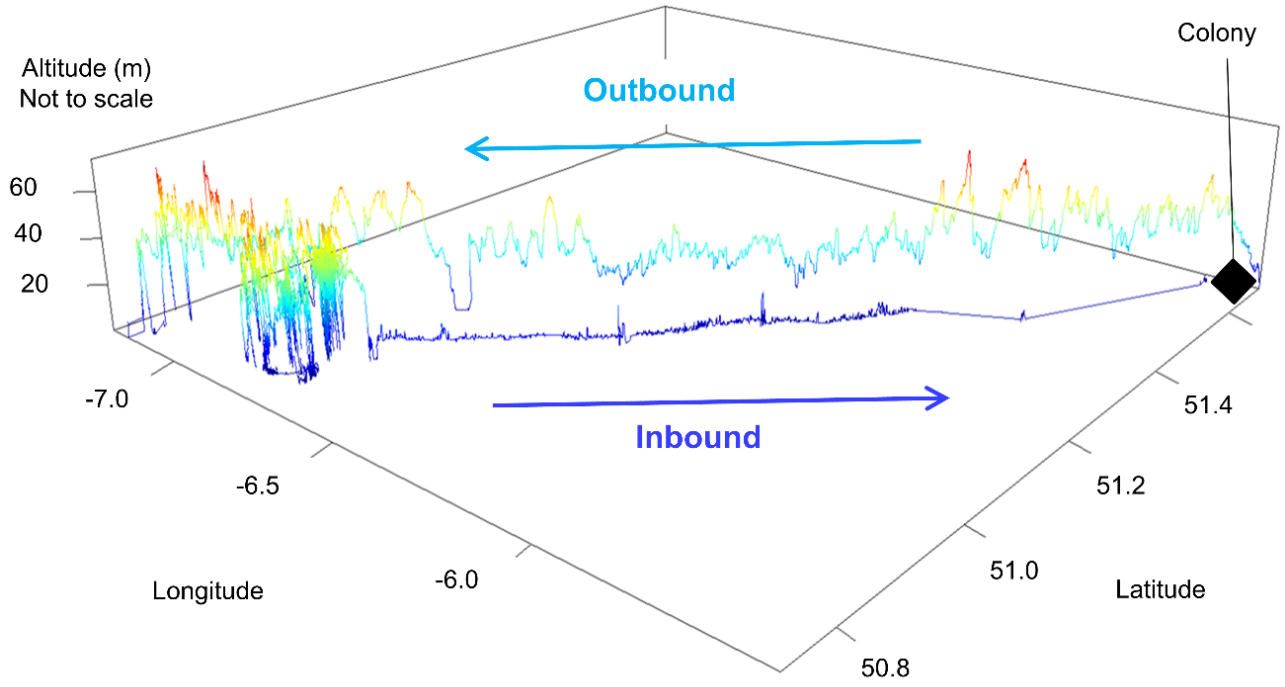


Figure 3.5. An example northern gannet *Morus bassanus* foraging trip plotted in three dimensions, with flight height derived from barometric pressure at 1hz frequency, and latitude and longitude derived from GPS at one-minute frequency. Colour represents altitude, with red being maximum and indigo showing sea level.

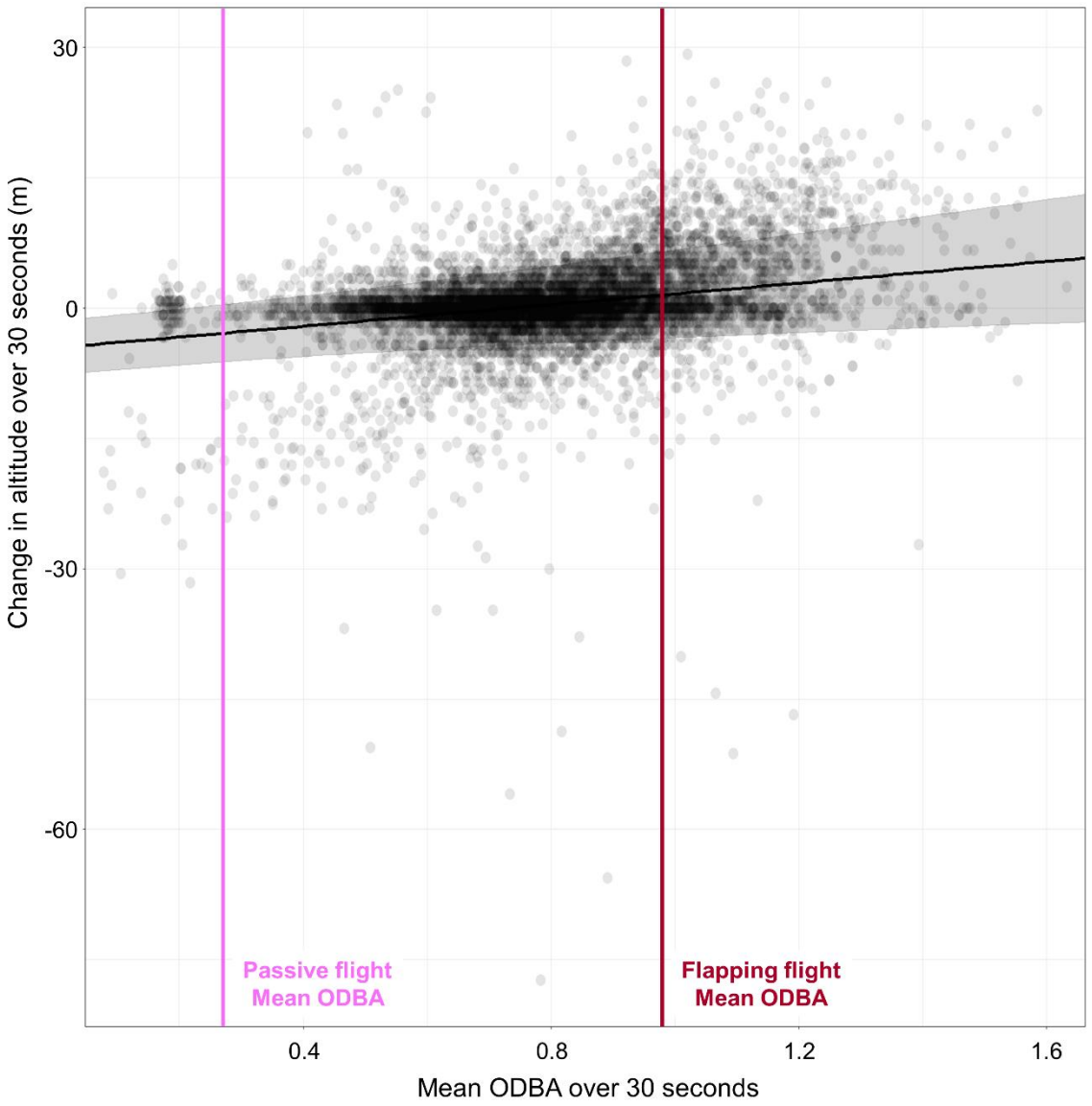


Figure 3.6. Relationship between mean ODBA and mean change in flight altitude over 7,974 30-second periods of continuous flight for eight northern gannets *Morus bassanus*. The black line shows the prediction from a Linear Mixed Model ± 95% confidence intervals with individual fitted as a random intercept and slope.

3.4.5 Comparing acceleration and GPS foraging metrics

The mean ± standard error was 28.5 hours ± 3.9 for trip duration, 105.9 km ± 8.4 for range, 363.4 km ± 33.0 for trip length, and 14.3 km/h ± 0.7 for mean speed. We compared metrics of foraging effort derived from accelerometry with those from GPS (Figure 3.7). Mean ODBA correlates only with mean speed (r = 0.77), while total ODBA correlates with trip duration (r = 0.74) and total distance (r = 0.65). Hours spent flying correlates most with distance travelled (r = 0.61) and hours spent resting correlates most with trip duration (r = 0.84).

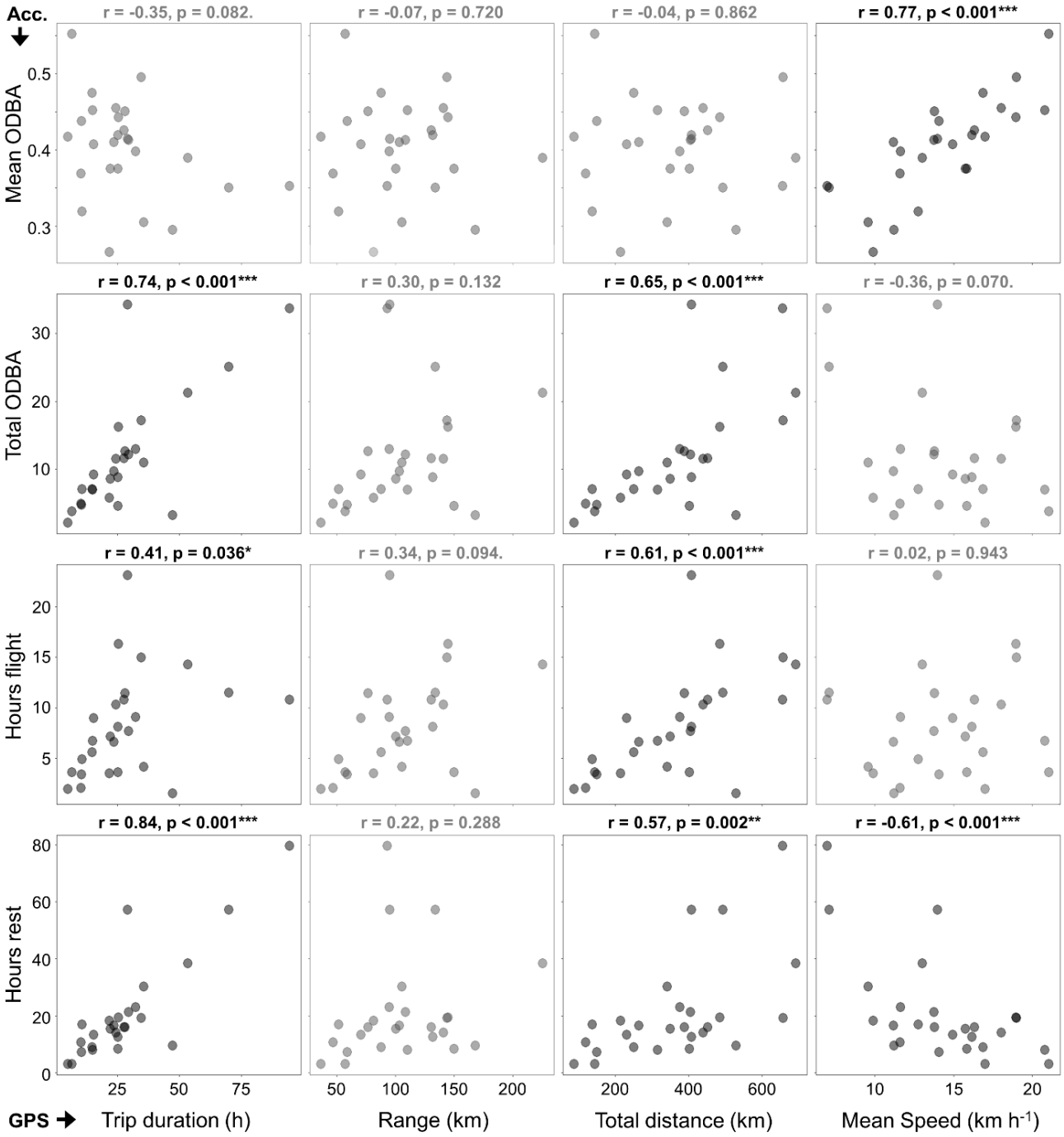


Figure 3.7. Comparison between metrics of foraging effort for northern gannets *Morus bassanus*, with each circle representing one foraging trip made by a unique individual. Correlations between four metrics of effort derived from acceleration data (mean trip ODBA, total trip ODBA, hours spent flying and hours spent resting), with four metrics derived from GPS data (trip duration, range (maximum distance from the colony), total distance travelled and mean speed). Black: $p < 0.05$, grey: $p > 0.05$.

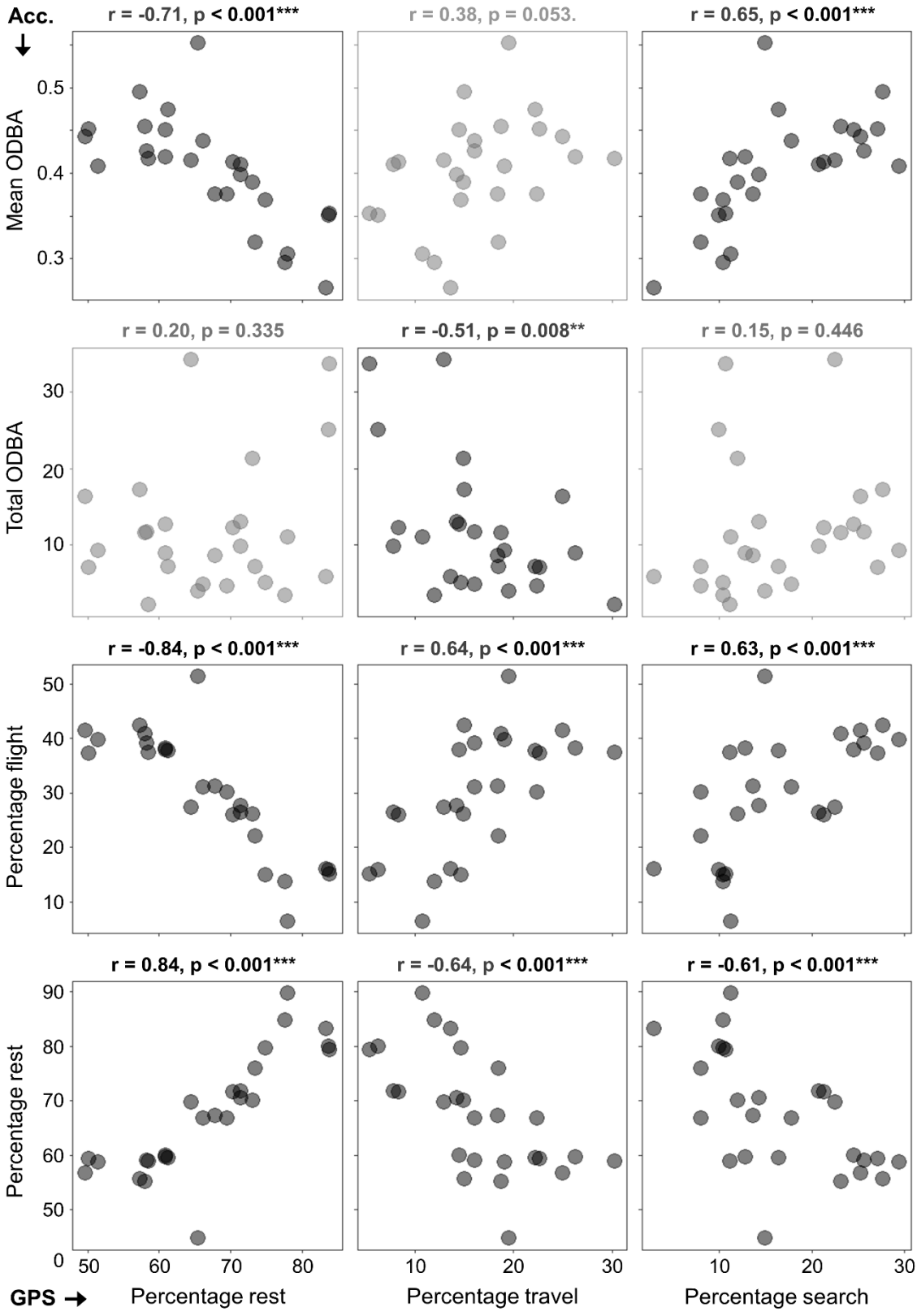


Figure 3.8. Comparison between metrics of foraging effort for northern gannets *Morus bassanus*, with each circle representing one foraging trip made by a unique individual. Correlations between four metrics of effort derived from acceleration data (mean trip ODBA, total trip ODBA, hours spent flying and hours spent resting), with three metrics derived from GPS data (percentage rest, travel or search). Black: $p < 0.05$, grey: $p > 0.05$.

3.5 Discussion

Video validated-accelerometry successfully identified the following behaviours: flapping flight, passive flight (gliding/soaring), plunge dive, takeoff and resting on the water. This provided accurate time budgets and calculations of energetic cost. While gannets travel long distances to bring back food for their chicks (363.4 km ± 33.0 standard error), they do not spend much of their foraging trips employing energy-saving gliding or soaring flight (only 28.5% of flight was passive). Flapping flight was the most energetically important behaviour in terms of mean ODBA (taking into account mean ODBA and time spent performing the behaviour). Most of the foraging trip was spent resting, and, consequently, this was the strongest predictor of the mean ODBA of a foraging trip (r = -0.90). There was a strong correlation between trip duration and both total ODBA (r = 0.74) and the time spent resting (r = 0.84), because the proportions of the trip spent resting were similar for trips of all durations, from five hours to 95. As a consequence of the conserved nature of these proportions and the mean ODBA for each behaviour (validated as a proxy for energetic expenditure for Australasian gannets using doubly labelled water; Angel, 2015), measures derived from GPS provide good metrics for foraging effort.

3.5.1 Energetic importance of each behaviour

Foraging trips lasted between 5.19 and 95.40 hours, with a mean of 29.96 ± 4.43 (Figure 3.3). The majority of foraging trips were spent resting on the water, which has the lowest mean ODBA at 0.21, with an average of 20.98 hours (67.5%). This contrasts with species, including other sulids, that return to land to rest every night (Lewis e*t al.,* 2004; Zavalaga *et al.,* 2012) and with species that travel for multiple days without landing by sleeping in flight (Liechti *et al.,* 2013; Rattenborg *et al.,* 2016).

Flight accounted for an average of 8.06 hours per trip (26.9%), consisting of short sections of flapping and passive flight (e.g. Figure 3.1). Flapping flight had the highest total ODBA (Table 3.3) and is therefore very important to overall effort as total ODBA accounts for time spent. Flapping flight had a mean ODBA of 0.98, nearly four times that of passive flight at 0.27 (gliding or soaring), and also accounted for a large part of the activity budget (20.5%), totalling 5.5 hours on average, with 68.2% of flight being classed as flapping flight. This supports previous studies showing that gannet species, despite their large wingspans,

have energetically costly flight styles (Birt-Friesen *et al.,* 1989; Green *et al.,* 2009). While gannets did use energy-saving passive flight (with an ODBA = 0.27, compared to 0.98 for flapping flight), the time spent in passive flight (8.7% ± 0.9 of the trip), is much less than flapping (20.5% ± 1.5) and does not vary much between individuals (Figure 3.3). This is a small proportion compared to species adapted for very low-cost flight, such as frigatebirds (Brewer & Hertel, 2007) and albatrosses (Sachs *et al.* 2012). Gannets are mainly flapping and gliding, rather than making use of air currents to soar for long periods as some other seabirds do, notably Procellariiformes, which use the wind-shear layers between waves (Richardson, 2011; Weimerskirch *et al.,* 2000). However, 28.5% of flight time represents a substantial energy saving compared to continuous flapping employed by some seabirds (Pennycuick, 1987) and other species (Bishop *et al.,* Vincze *et al.,* 2019). Passive flight had an ODBA almost as low as resting on the water (Table 3.3), and gannets change their heart rate even when switching between short periods of flapping and passive flight (Ropert-Coudert *et al.,* 2006).

Takeoff was by far the costliest behaviour per unit time (mean ODBA = 2.36; Table 3.3; Figure 3.2) and often formed part of foraging bouts characterised by repeat take-off and diving, presumably associated with productive prey patches (e.g. fish schools, fishing vessels). However, takeoff only accounts for an average of 4.6 minutes per foraging trip (0.3%), so it is not a major cost overall (1.5% of mean total ODBA). Plunge dives also had a relatively high mean ODBA (1.78). Nevertheless, this is unlikely to accurately reflect energetic expenditure because the acceleration is generated by gravity during the characteristic plunge dive. However, the total ODBA will not be affected much because the aerial part of the plunge dive only accounts for an average of 1.6 minutes per foraging trip (0.1%).

While the foraging trips differed substantially in length, the proportion of time spent carrying out each activity was much more consistent between individuals (Figure 3.3; Figure 3.7). The mean ODBA for each behaviour was also consistent between individuals for flapping flight, passive flight, rest on water and active on water, but more variable for takeoff and plunge dive. We found that individuals were fairly consistent in the costs relating to each behaviour (Figure 3.2), and the mean ODBA of any particular behaviour was not strongly correlated with the mean ODBA for the entire trip (Figure 3.4). The mean ODBA was instead driven by the percentage of time spent performing each behaviour, being strongly

negatively related to time spent resting, and positively related to time spend in flapping flight, takeoff and plunge dive (Figure 3.4). As such, it appears that the energetic expenditure for gannets is driven by time spent active, and not by differences in the effort required to travel or forage per unit time.

3.5.2 Flight costs and altitude

There is a significant positive relationship between ODBA and altitude change (Figure 3.6). However, the slope is shallow, and there is a large amount of variation, mostly within individuals (Figure S3.5). This shows that the cost of gaining altitude is variable. This is likely due to external factors such as wind conditions (Amélineau *et al.,* 2014; Elliott *et al.,* 2014; Weimerskirch *et al.,* 2012), and so further study should incorporate wind conditions as these are known to influence the foraging trips of seabirds, including gannet (Amélineau *et al.,* 2014). Furthermore, the cost of gaining altitude is likely to relate to which birds are travelling or searching because altitude gain is required both to increase plunge dive depth (Garthe *et al.,* 2014), and potentially gain a better viewpoint (Andersson *et al.,* 2009). We also observed a small number of cases of flight in formation with other gannets, which is likely to provide aerodynamic energetic savings (Portugal *et al.,* 2014).

3.5.3 Comparing acceleration and GPS foraging metrics

The metrics of foraging effort derived from GPS correlated with those derived from acceleration (Figure 3.7). Mean speed was the best indicator or mean ODBA ($r = 0.77$), which shows how hard the bird was working per unit time. Trip duration was the best indicator of total ODBA ($r = 0.74$), because trips did not vary much in the hours spent resting ($r = 0.84$) and resting makes up 67% of the average trip. Total distance travelled was the best correlate of hours spent flying ($r = 0.61$). Foraging range was not significantly correlated with any metric derived from acceleration, the highest being hours spent in flight ($r = 0.34$). As such, trip duration appears to be the best indicator of overall foraging effort, followed by total distance. Furthermore, methods for classifying behaviours from GPS using speed and tortuosity were effective in identifying resting behaviour when compared to accelerometry ($r = 0.84$, $p < 0.001$; Figure 3.8). Validating the use of GPS-derived metrics of foraging effort is useful because acceleration data is

not available for many studies of foraging effort for gannets and other sulids (Bertrand *et al.,* 2012; Mullers & Navarro, 2010; Pettex *et al.,* 2012).

3.6 Conclusion

Video-validated accelerometry provided accurate behavioural time budgets and calculations of the relative energetic expenditures of particular behaviours. This showed that gannets spend most of their time on foraging trips resting, but when they are active, most of their flight is costly flapping flight. Consequently, flapping flight makes the largest contribution to the total energetic cost of foraging trips. Gannets work harder to gain altitude, but there is much variation, indicating that the cost of gaining altitude is variable. The energetic expenditure involved in each behaviour is generally consistent among individuals, with the overall energetic cost of the trip driven by the relative time spent performing each behaviour. Time spent performing each behaviour was fairly consistent between individuals and independent of trip duration. This meant that foraging trip duration and distance travelled correlated well with total ODBA, highlighting their reliability as metrics of total foraging effort. Furthermore, mean speed correlates well with mean ODBA, providing a good metric for effort per unit time. Good indices of foraging effort can then be used to investigate the causes of variation, such as prey availability and competitive pressure.

3.7 Supplementary material

Figure S3.1 shows the logger attachment method. Figure S3.2 presents variable importance for the random forest model for classifying behaviours from acceleration data. Table S3.1 details the logic-based corrections for behaviour labels applied to acceleration data using a video-validated random forest model. Figure S3.3 shows examples of visual assessment of errors made by a random forest model to classify behaviours from acceleration data. Table S3.2 provides the visually assessed error rate in behavioural classification from acceleration data for each bird. Table S3.3 and Figure S3.4 show sex differences in the mean and total ODBA for each behaviour. Figure S3.5 shows the variation between and within individuals in the ODBA for 30-second periods of flight.

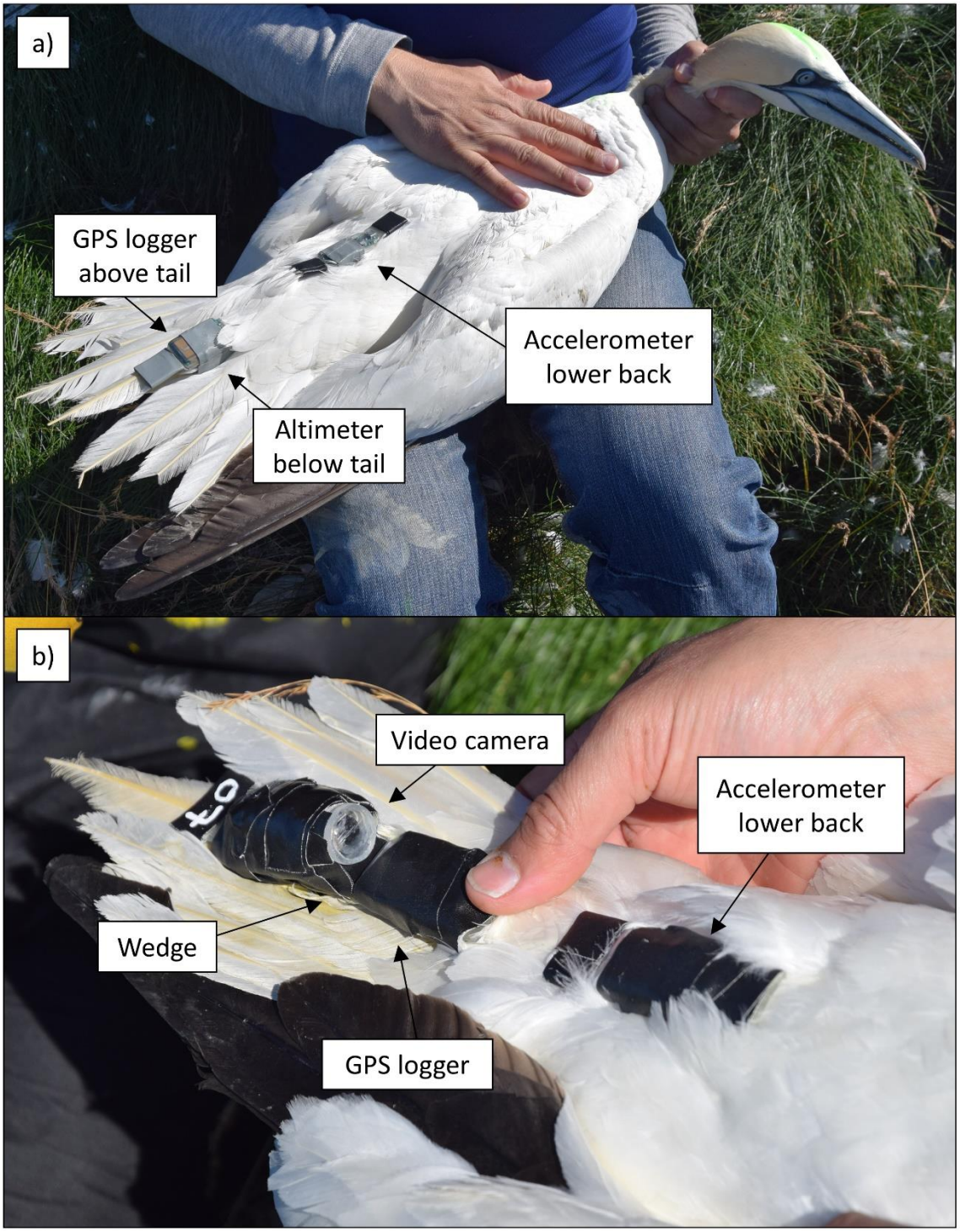


Figure S3.1. Photographs showing the attachment methods using Tesa® 4651 tape for the combined deployment of GPS loggers, accelerometers and a) altimeters or b) video cameras. Tail-mounted loggers were attached to the central four tail feathers, and back-mounted loggers were placed along the central line as far back as possible while avoiding the preen gland.

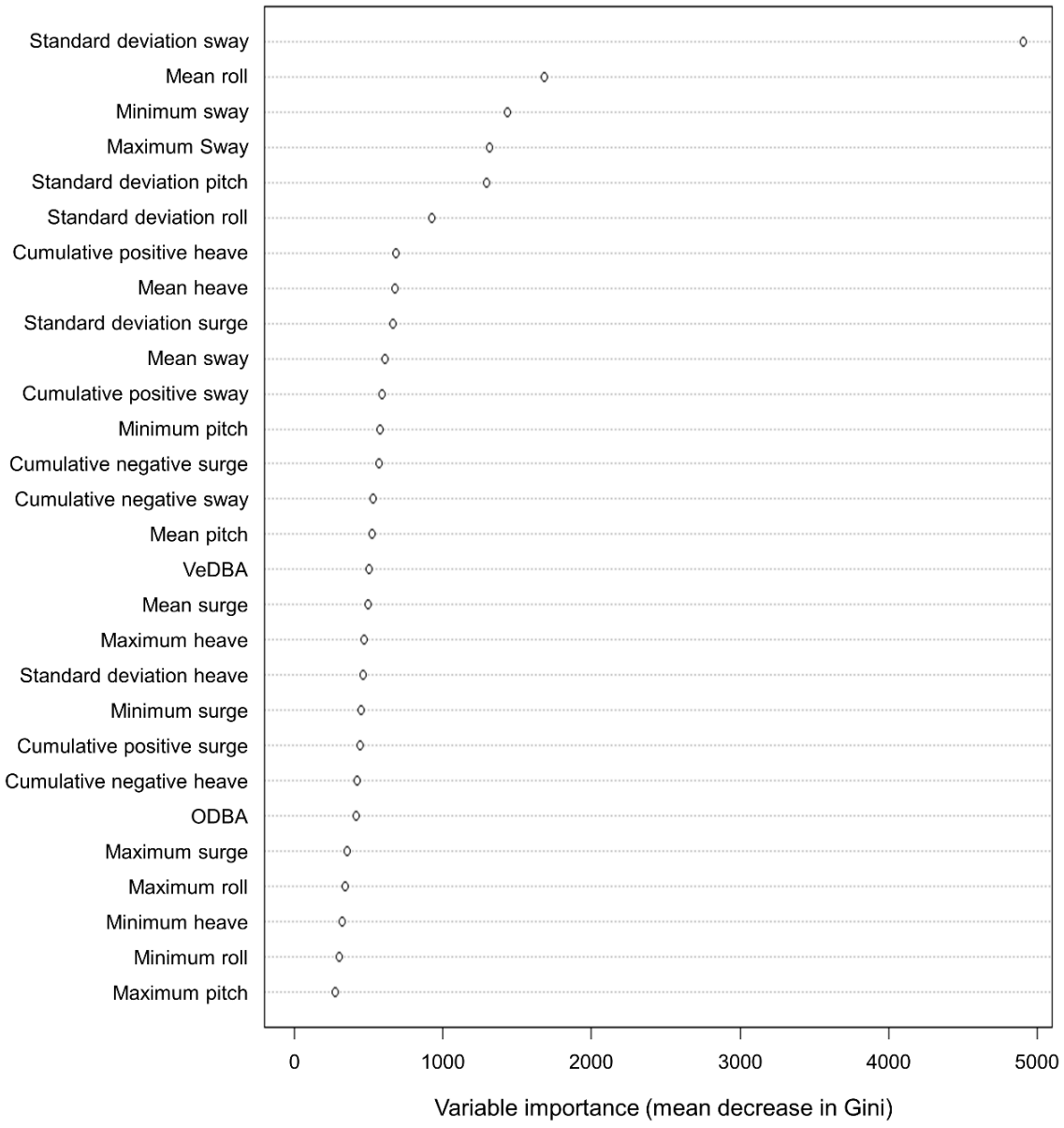


Figure S3.2. Variable importance plot for the random forest model for classifying gannet behaviours from tri-axial acceleration data, with a higher score indicating a greater importance of a variable for correctly labelling records. Each variable is generated from 100 acceleration records at 50hz (two seconds) using one or more of the surge (x), sway (y) and heave (z) axes.

Table S3.1. Logic correction based on previous and next behaviours in a time series for labels generated by a video-validated accelerometry implemented using a random forest model. For example, if the focal behaviour is labelled as rest on water or preen and the next and previous behaviours are flapping or passive flight, the focal behaviour was relabelled as 'unknown flight' because it is not possible to transition from water to flight and back to water between two-second segments.

	Behaviour			
	Focal	Previous	Next	Corrected to
Level 1	Flapping flight	Rest on water Preen Underwater Land on water	Rest on water Preen Underwater Land on water	Preen
	Passive flight	Rest on water Preen Underwater Land on water	Rest on water Preen Underwater Land on water	Rest on water
	Rest on water Preen Underwater Land on water	Flapping flight Passive flight	Flapping flight Passive flight Dive	Unknown flight
	Rest on water Preen Underwater Land on water	Takeoff	Flapping flight Passive flight	Unknown flight
Level 2	Flapping flight Passive flight Unknown flight	Rest on water Preen Underwater Land on water	Rest on water Preen Underwater Land on water	Rest on water
	Rest on water Preen Underwater Land on water	Flapping flight Passive flight Unknown flight	Flapping flight Passive flight Unknown flight	Unknown flight
	Rest on water	Dive	Rest on water	Preen

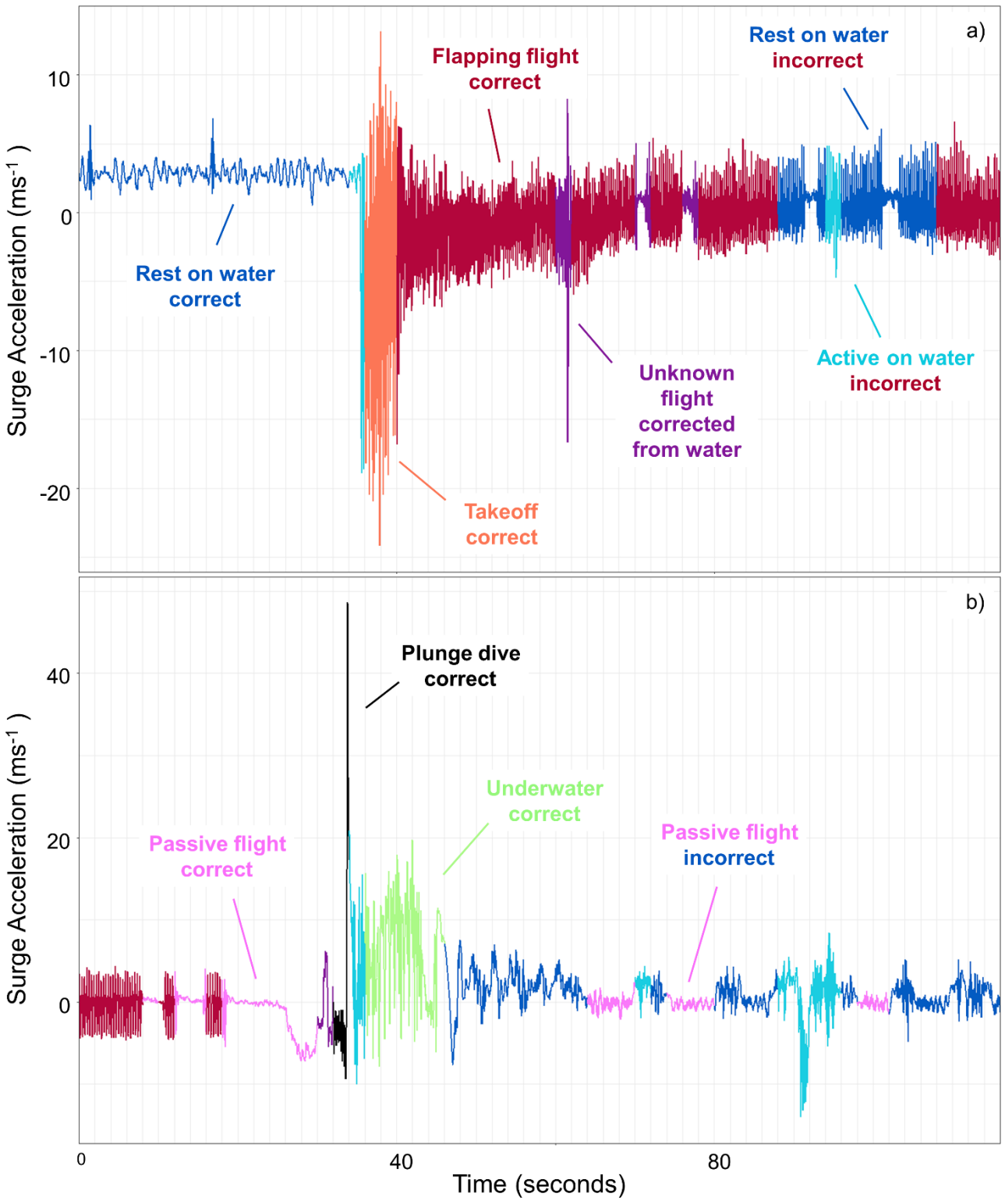


Figure S3.3. Acceleration data in the surge axis showing examples of visual assessment of errors from the context of the surrounding behaviours, showing, a) when a section of flight is incorrectly labelled as resting or active on the water (ten errors), and, b) water is labelled as flight (eight errors).

Table S3.2. Visually assessed errors from plotting logic-corrected random forest model predictions. *Birds included in the training dataset. There were 21,083 errors across 1,402,250 records for 26 birds (1.50%). Of the recorded errors, 58.1% were flight behaviours (flapping/passive) labelled as water (water/preen/underwater), and 39.5% were water labelled as flight. There were 32 dives missed and 386 added.

Bird ID	Errors	%	Main error	Dives missed	Dives added
G409	39	0.07	Water labelled as flight	0	1
G413	21	0.17	Flight labelled as water	0	1
G415	17	0.04	Water labelled as flight	0	1
G435	1109	0.75	Water labelled as flight	1	211
G439	1644	3.25	Water labelled as flight	0	3
G441	2475	3.74	Water labelled as flight	3	0
G442	2216	7.97	Water labelled as flight	0	23
G444	70	0.18	Water labelled as flight	1	6
G445	3885	6.18	Flight labelled as water	3	17
G446	179	0.79	Preen labelled as dive	0	71
G447	142	0.37	Flight labelled as water	0	2
G448	203	0.75	Flight labelled as water	0	1
G449	7	0.07	Water labelled as flight	0	1
G450	1	0.003	Land/dive labelled as preen	1	0
G473*	59	0.14	Water labelled as flight	4	2
G474*	217	0.98	Water labelled as flight	2	0
G476*	284	0.29	Flight labelled as water	6	0
G481	10	0.05	Preen labelled as dive	0	5
G484*	9	0.05	Flight labelled as water	0	1
G485*	7003	4.08	Flight labelled as water	1	11
G491*	715	1.68	Water labelled as flight	0	1
G495*	133	0.10	Water labelled as flight	0	1
G496*	276	0.61	Flight labelled as water	0	1
G502*	325	0.52	Water labelled as flight	4	0
G504*	105	0.21	Water labelled as flight	1	0
G506	150	0.28	Flight labelled as water	5	26

Table S3.3. Estimates ± standard errors across 12 female and 14 male northern gannets *Morus bassanus* foraging trips for mean and total Overall Dynamic Body Acceleration (ODBA) is the mean ODBA multiplied by the time in hours (estimates given for males relative to females).

Behaviour	Total ODBA	Mean ODBA
All behaviours	Est. = 2.647 ± 3.486, $\chi^2_{1,24}$ = 0.574, p = 0.449	Est. = -0.004 ± 0.026, $F_{1,24}$ = 0.024, p = 0.878
Flapping flight	Model checks failed, (p = 0.436)	Est. = -0.032 ± 0.028, $F_{1,24}$ = 1.375, p = 0.252
Water rest	Est. = 0.882 ± 1.742, $\chi^2_{1,24}$ = 0.255, p = 0.614	Est. = -0.007 ± 0.009, $F_{1,24}$ = 0.518, p = 0.479
Water active	Model checks failed, (p = 0.742)	Est. = -0.049 ± 0.028, $F_{1,24}$ = 3.053, p = 0.093
Passive flight	Est. = 0.229 ± 0.177, $F_{1,24}$ = 1.664, p = 0.209	Est. = 0.019 ± 0.024, $F_{1,24}$ = 0.650, p = 0.428
Takeoff	Est. = 0.044 ± 0.050, $\chi^2_{1,24}$ = 0.772, p = 0.380	**Est. = -0.257 ± 0.102, $F_{1,24}$ = 6.357, p = 0.019***
Plunge dive	Est. = 0.0009 ± 0.018, $\chi^2_{1,24}$ = 0.003, p = 0.959	Est. = -0.083 ± 0.110, $F_{1,24}$ = 0.568, p = 0.458

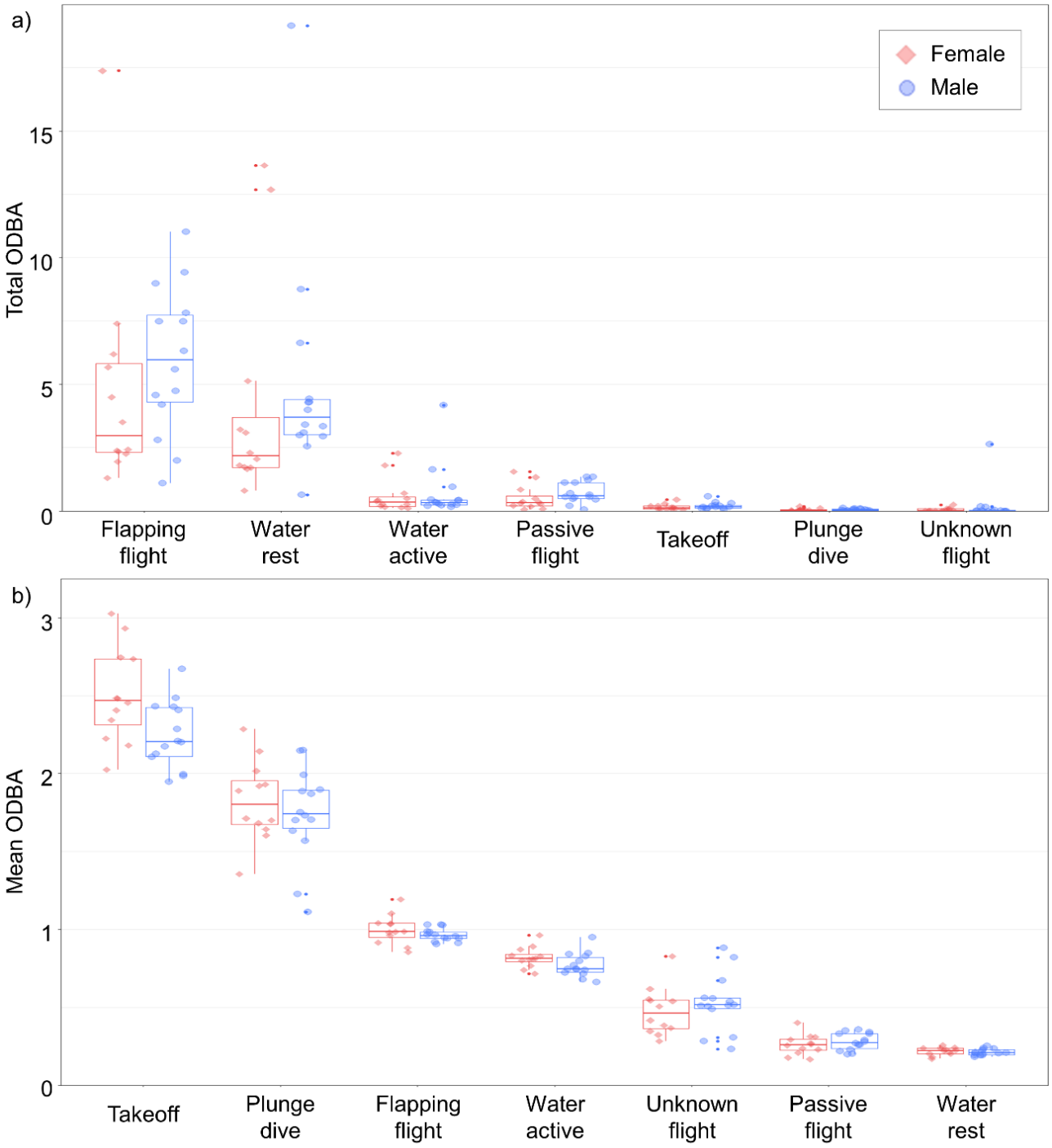


Figure S3.4. The a) total and b) mean Overall Dynamic Body Acceleration (ODBA) for each behaviour performed by northern gannets *Morus bassanus* separated by sex. Each jittered circle shows the mean for an individual across one foraging trip. The total ODBA is the mean ODBA for each behaviour multiplied by the hours spent performing it.

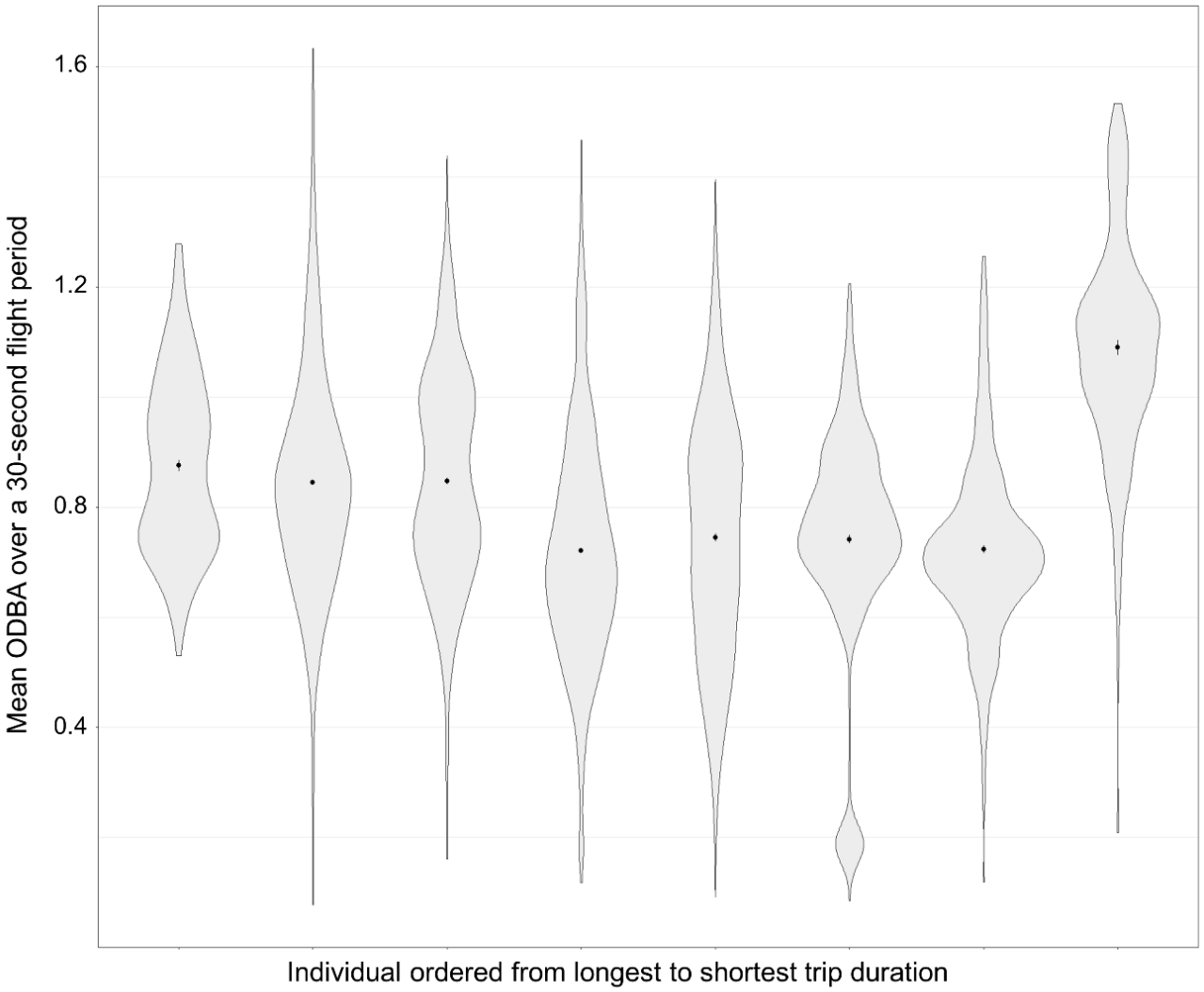


Figure S3.5. Distributions (grey) and means (black circle) for mean Overall Dynamic Body Acceleration (ODBA) over 30-second flight periods for eight individual gannets used in the analysis of ODBA in relation to altitude (Figure 3.6).

Chapter 4 – The ecology of scavenging: Multi-logger deployments reveal the incidence and implications of feeding on fishery waste

4.1 Abstract

Anthropogenic food sources have major ecological and evolutionary impacts, but the ecology of scavenging is poorly understood. Convention suggests that predictable anthropogenic food subsidies are easier to access than natural foods, but few studies describe scavenging in detail, and fewer still quantify energy expenditure during this type of foraging. Fisheries waste is one of the biggest subsidies, but bans are reducing discard availability in many regions, including in the EU. Here we assess the incidence and implications of scavenging from fishing vessels for a wide-ranging marine predator, the northern gannet *Morus bassanus*, in the UK. We used bird-borne video cameras to differentiate scavenging from natural foraging, and time-matched GPS and accelerometer data to assess how gannets exploit vessels and the energetic expenditure relative to natural foraging. Scavenging was common; of 272 dives performed by 37 individuals, 55% occurred at vessels. Individuals were repeatable within the recorded period (mean 3.9 hours), with 46% diving only at vessels, 40.5% diving only naturally and 13.5% employing both strategies. Scavenging incidence did not differ significantly between years or sexes. Videos revealed prey capture events, showing that gannets acquired food in different ways at fishing boats: some collected discards while others took fish directly from trawl nets below the surface. There were no differences in effort between scavenging and natural foraging in terms of dive frequency, foraging range, trip duration, distance travelled, mean speed or mean overall dynamic body acceleration (ODBA: a proxy for energy expenditure), total ODBA (mean ODBA multiplied by duration), time spent active or percentage of the trip spent active. Gannets collected discards from the surface, but more commonly performed a costly series of takeoffs and plunge dives at the same vessel, like when foraging on shoals of fish. Overall, gannets in the Celtic Sea hunt natural prey, but also regularly use fisheries, with no difference in energetic expenditure between these strategies. Gannets obtain food from fishing vessels that are not discarding, but the loss of fisheries waste as a food source is likely to impact a subset of scavengers (57% of sampled individuals), particularly during times of low natural prey availability.

Keywords: subsidies; discards; accelerometry; animal-borne cameras; dynamic body acceleration; anthropogenic resources; human-provided food; predictable anthropogenic food subsidies (PAFS)

4.2 Introduction

A wide range of species exploit human-provided resources with major ecological and evolutionary consequences (Oro *et al.,* 2013). Predictable anthropogenic food subsidies (PAFS) shape ecosystems by increasing survival (Brittingham & Temple, 2018) and breeding success (Oro, Bosch & Ruiz, 1995), leading to changes in population density (Fedriani, Fuller & Sauvajot, 2001), morphology (Yom-Tov, 2003) and genetic diversity (Agudo *et al.,* 2010). As well as increasing the total amount of available food, subsidies can reduce foraging effort due to their predictability (García-Tarrasón *et al.,* 2015) and easier handling or capture compared with natural foods (Oro *et al.,* 2013). This can reduce time spent foraging (Bartumeus *et al.,* 2010) and home range size (Bino *et al.,* 2010). However, accessing anthropogenic foods may increase human-wildlife conflict (Beckmann & Lackey, 2008) and scramble competition between scavengers (Arcos, Oro & Sol, 2001), or reduce diet quality (Österblom *et al.,* 2008). Understanding how animals use subsidies and how this behaviour is distributed within populations is key to predicting the impact of rapid food losses caused by changes in human behaviour or policy (Furness, 2003; Pons & Migot, 1995), such as food waste prevention measures (FAO, 2011; Newsome & van Eeden, 2017). While many studies show that PAFS are important, their influence is poorly understood at the individual level (Oro *et al.,* 2013). In particular, impacts will depend on whether scavengers are generalists or specialists (Newsome *et al.,* 2015). Moreover, foraging effort may be lower for scavenging, but few studies measure this directly (Fehlmann *et al.,* 2017; Granadeiro *et al.,* 2011).

Fisheries provide one of the three main sources of PAFS worldwide (Oro *et al.,* 2013), and like many marine top predators, seabirds are a beneficiary (Bicknell *et al.,* 2013; Votier *et al.,* 2008). A least 52% of seabird species scavenge from fishing vessels, including populations for which fisheries waste can make up 75% of their diet (Oro *et al.,* 2013). Populations artificially inflated by subsidies are vulnerable to sudden losses (Fondo *et al.,* 2015; Oro *et al.,* 1995). However, efforts to improve the sustainability of fisheries have reduced the availability of discards (Zeller & Pauly, 2005). As the fishing industry unsustainably exploits marine fish populations around the globe (Halpern *et al.,* 2008; Pauly *et al.,* 1998), discard bans are now planned or implemented in many regions, including the European Union, Iceland, Norway, Chile and New Zealand (Commission of European Communities, 2009; Marchal *et al.,* 2016; Popsescu &

Poulsen, 2012). As such, understanding how discards affect seabird foraging behaviour, population dynamics and community structure is a research priority (Lewison *et al.,* 2012).

To predict the impact of changes in discarding practice or policy, it is crucial to determine precisely how seabirds exploit vessels, particularly through mechanisms other than collecting discards such as feeding from trawler nets (Petyt, 1995). Furthermore, little is known about the relative effort required to scavenge compared to hunting naturally. Effort could be lower due to the ease of locating fishing vessels and collecting dead or stunned fish compared to live prey, but scramble competition at boats may negate any energetic savings in terms of prey handling (Arcos *et al.,* 2001). Furthermore, fishing gear may present a high risk of mortality through collision, hooking on lines or entanglement (Gianuca *et al.,* 2017), and, scavenged fish can have poor nutritional quality, so larger meals may be required to sustain adults or chicks (Grémillet *et al.,* 2008; Österblom *et al.,* 2008; Pichegru *et al.,* 2007).

Here we provide one of the most detailed studies of scavenging behaviour at the individual level. We investigate fishing vessel exploitation among chick-rearing northern gannets *Morus bassanus* (hereafter “gannets”). Gannets regularly scavenge from fishing boats (Votier *et al.,* 2013) and have a high energetic cost of foraging (Birt-Friesen *et al.,* 1989; Green *et al.,* 2009). We combine bird-borne video cameras, GPS loggers and accelerometers to investigate foraging behaviour in fine detail. First, we quantify the incidence of scavenging in terms of the proportion of dives occurring at fishing vessels, how this varies with year and sex, and test for individual repeatability in scavenging within the recorded period of the foraging trip. Second, we investigate the precise technique of foraging at boats in terms of where prey is taken during discarding or net hauling. Third, we compare the foraging effort of scavenging and natural foraging.

4.3 Methods

4.3.1 Study site and sampling

Fieldwork took place in July and August of 2016 and 2017 on Grassholm Island, UK (51º43'N, 05º28'W), an offshore gannet colony of 36,011 breeding pairs in 2015 (Murray, Morgan & Harris, 2015). We captured chick-rearing gannets using a pole and crook during the changeover between adults at the nest, ensuring that chicks were not unattended and foraging trips began immediately after release. We equipped birds with video cameras (Perthold Engineering BirdCam, 24g), GPS loggers (Mobile Action Technology i-gotU 120, 18g), and tri-axial accelerometers (Gulf Coast Data Concepts X16-mini, 16g). We attached GPS loggers and cameras to the central tail feathers using Tesa® 4651 tape, with the camera on top of the tail facing towards the head at a slightly elevated angle. We taped accelerometers to the lower back feathers to more accurately reflect body movement and reduce the impact on flight by spreading logger weight toward the centre of gravity (Vandenabeele *et al.,* 2014). The combined logger weight of 58g was 2.0% of the mean weight of tagged birds (2850g) and 2.4% of the lightest (2450g). We recaptured birds after at least one foraging trip to recover the loggers. Previous studies detected no effects of similar loggers (20g, 30g and 70g) on the foraging trip duration or body mass of chick-rearing gannets (Hamer *et al.,* 2007, 2009; Lewis *et al.,* 2002). We fitted all individuals with a metal ring and multi-layered impact acrylic leg ring engraved with a four-digit alphanumeric code (http://colour-rings.eu) for re-sighting, and to aid recapture, we marked them with non-toxic animal dye (All-Weather Paintstik). For molecular sexing, we took a blood sample of 1–2ml from the tarsal vein using 23–25-gauge needles. Protocols were completed under licence from Natural Resources Wales (22478:OTH:SB:2010), the British Trust for Ornithology (BTO: A4257), the BTO Special Methods Panel and the UK Home Office (30/3065).

4.3.2 GPS data

GPS loggers were set to record a fix every minute. We time-matched the GPS data to the video footage and extracted the first complete foraging trip (where birds left a radius of 200m from the centre of the colony). We recorded trip duration, and calculated distance travelled and range using the 'geosphere' R package (Hijmans, 2017). To calculate mean speed, we divided distance travelled by trip duration.

4.3.3 Video data

Cameras were programmed to record 30 minutes of footage followed by 30 minutes on standby until the battery failed, which averaged 3.9 hours of footage across approximately nine hours from deployment. We coded videos for the following five behaviours: 1) flight, 2) plunge dive, 3) underwater, 4) land on water and 5) rest on water, partly using BORIS video coding software (Friard & Gamba, 2016). For each bird, we recorded the total number of dives with and without fishing vessels. For each dive, we also recorded the duration (to the nearest second). For a subset of dives, we observed the foraging technique (e.g. “capture of live fish”, “dive next to discards chute”, “dive next to trawl net during hauling”).

4.3.4 Acceleration data

Accelerometers recorded continuously at 50hz. We extracted acceleration data using the trip start and end times recorded by the GPS loggers. We calculated overall dynamic body acceleration (ODBA) as a proxy for energy expenditure (Halsey *et al.,* 2008; Halsey, Shepard & Wilson, 2011; Wilson *et al.,* 2006), which has been validated using doubly-labelled water for the closely-related Australasian gannet *Morus serrator* with correlation of $r^2 = 0.63$ with VeDBA (Angel, 2015). We used the video data to create a training dataset of two-second sections. For each section, we calculated summary metrics and used a random forest model to categorise the behaviours. We applied a logic correction based on the previous and following behaviours for each two-second period (see Chapter 3). We calculated total ODBA as mean ODBA multiplied by duration. As resting on the water accounts for the majority of gannet foraging trips, we calculated the time and percentage time spent active.

4.3.5 Statistical analysis

We used binomial General Linear Models to investigate the effect of sex and year on scavenging incidence (i.e. scavenging or natural foraging as the response variable). As gannet foraging trips can vary in distance, duration and location between sexes (Cleasby *et al.,* 2015b; Stauss *et al.,* 2012) and years (Hamer *et al.,* 2007; Warwick-Evans *et al.,* 2016a), we included these variables in all models. For whole trip analysis, we classed the foraging trip strategy as “scavenging” if over 50% of dives were performed at vessels, with the remaining trips classified as “natural foraging”. We analysed foraging range, mean speed,

mean ODBA and the percentage of time spent active in relation to the foraging strategy, sex and year, using Linear Models (LM). We analysed dive frequency, trip duration and total distance travelled, total ODBA and time spent active in relation to the foraging strategy, sex and year, using General Linear Models (GLM) using gamma distributions with identity links. We performed all data processing and statistical modelling in R (R Core Team, 2017).

4.4 Results

4.4.1 Incidence of scavenging

We recorded 152.3 hours of video footage across 39 individuals (mean 3.9 hours), with footage for 37 birds containing 351 dives. We observed that 59.5% of dives occurred at fishing vessels, while the remaining 40.5% were natural foraging events, occurring alone or with conspecifics and/or other predators, such as common dolphins *Delphinus delphis* (Table 4.1; Figure 4.1). The incidence of natural or vessel dives was highly repeatable within foraging trips: 17/37 (45.9%) of individuals dived only at vessels, 15 (40.5%) dived only away from vessels, and five (13.5%) dived both with and without vessels during the recorded period (Figure 4.1). Scavenging accounted for 56.8% of foraging trips (Table 4.1). There were higher proportions of scavenging dives and trips in 2017 compared to 2016, although this was not statistically significant, and similar proportions for females compared to males (Table 4.1).

Table 4.1. Incidence of northern gannet *Morus bassanus* dives at vessels, and foraging trips classed as scavenging (>50% of dives occurred at fishing vessels) or natural foraging, with test statistics from Binomial General Linear Models coded as: event (dive/trip) ~ year + sex. The number shows the order in which variables were removed (1 = first, 2 = last) using backwards stepwise deletion.

Event	Group	Natural	Scavenging		Scavenging est.±SE	χ^2	d.f.	p
Dives	All	142	209	(59.5%)	-	-	-	-
	2016	55	49	(47.1%)	2: 19.966 ± 3.927	3.044	1	0.081.
	2017	87	160	(64.8%)				
	Female	50	88	(63.8%)	1: -0.039 ± 2.787	0.0002	1	0.989
	Male	92	121	(56.8%)				
Trips	All	16	21	(56.8%)	-	-	-	-
	2016	9	8	(47.1%)	2: 0.737 ± 0.675	1.209	35	0.272
	2017	7	13	(61.9%)				
	Female	6	10	(62.3%)	1: -0.400 ± 0.687	0.342	34	0.559
	Male	10	11	(52.4%)				

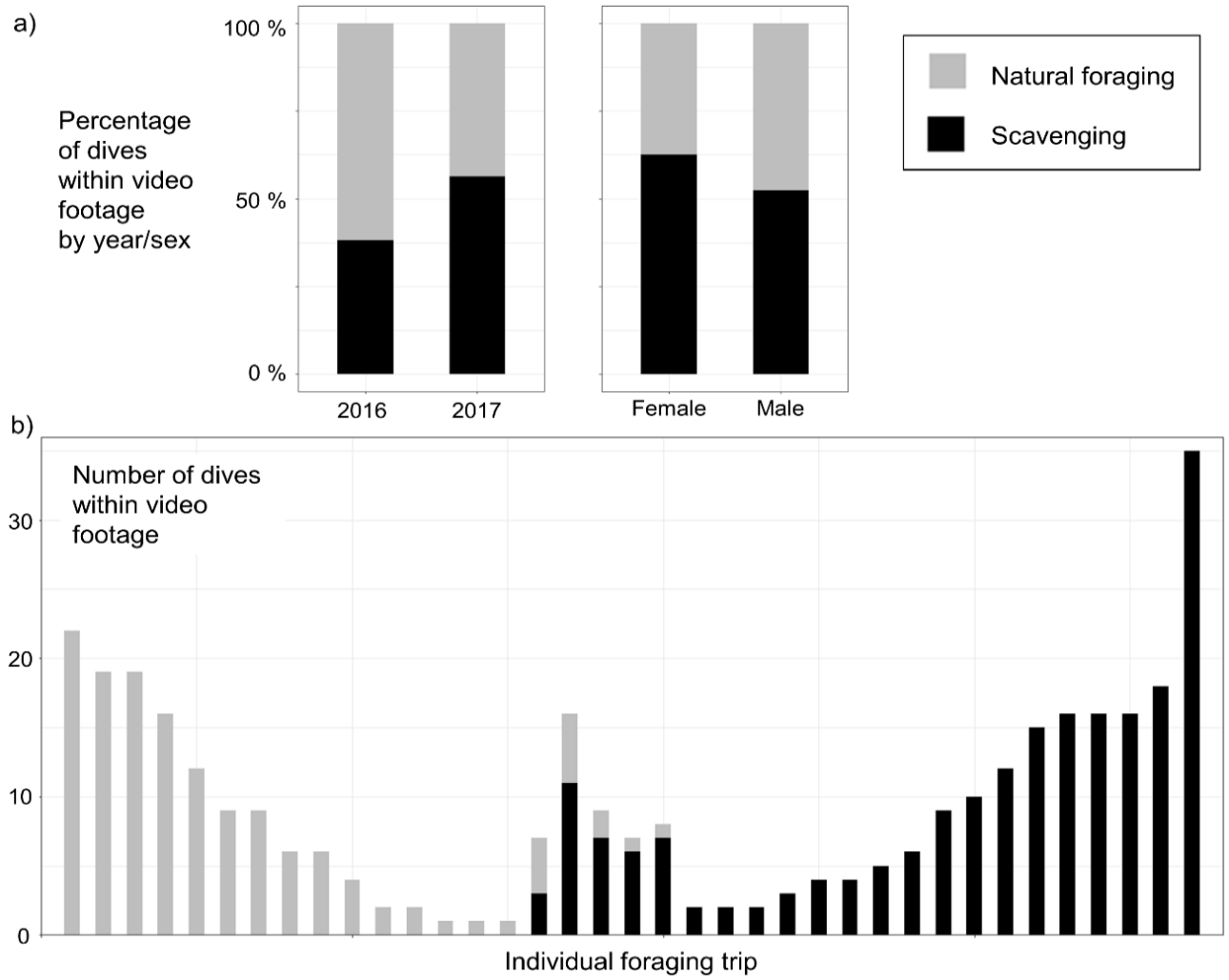


Figure 4.1. Incidence of northern gannet *Morus bassanus* scavenging and natural dives across a) years and sexes, and b) individuals, where each bar represents an individual. See Table 4.1 for summary values.

4.4.2 Scavenging technique

Gannets foraged at fishing vessels using two strategies: 1) on discards/offal and 2) during trawler net hauling (Figure 4.2). It was not possible to distinguish the difference between discards and offal. When feeding on discards/offal, gannets either took them from the surface and or plunge dived into the water column. When taking fish during hauling, gannets were also able to glean prey from the surface, and, by plunge-diving, they were able to take fish attached to the outside of the net or take catch through the mesh (Figure 4.2d, 4.2e).

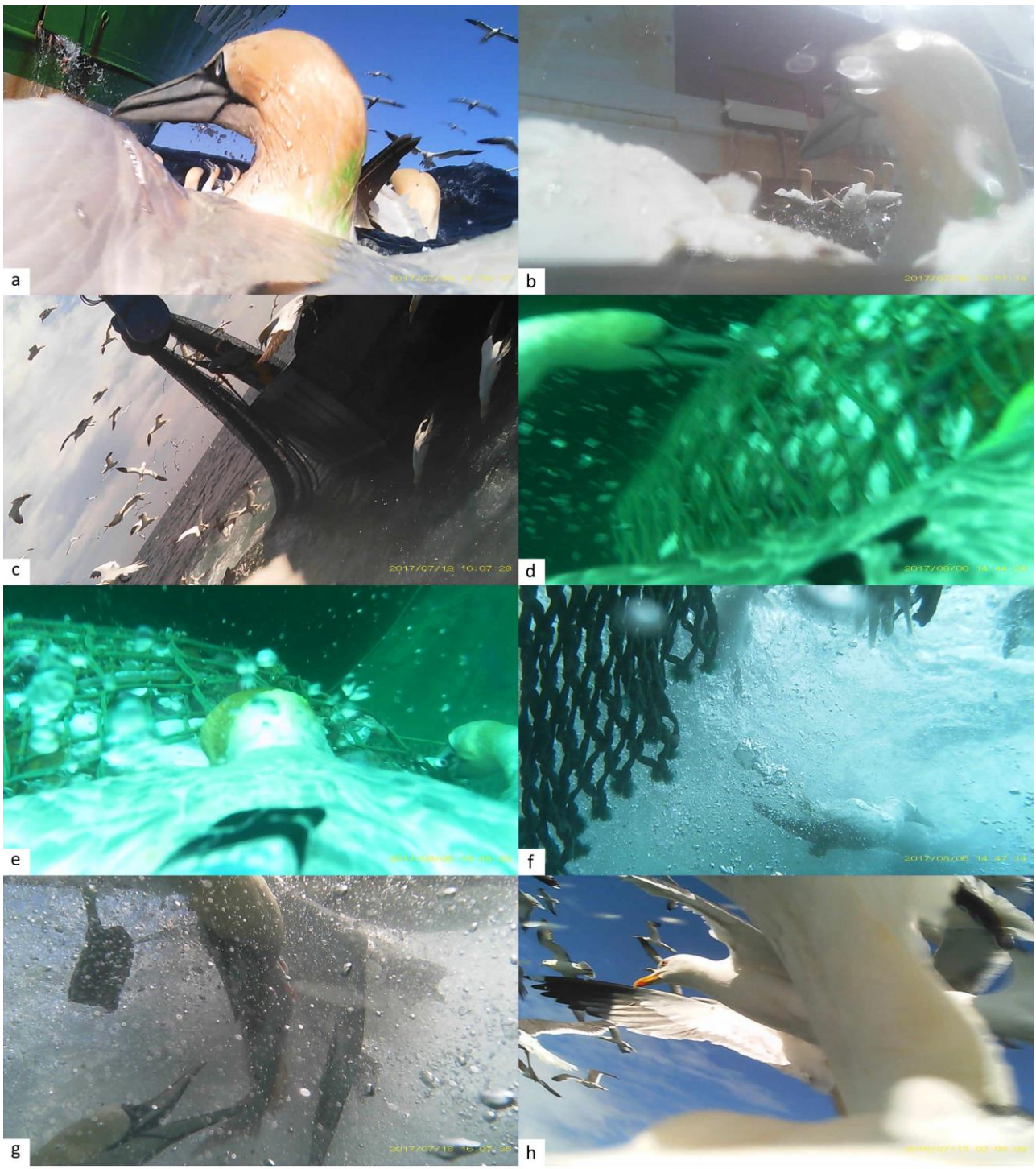


Figure 4.2. Example images from bird-borne video cameras showing scavenging behaviour in northern gannets *Morus bassanus* from Grassholm, UK. Foraging next to active discards chutes on a) small and b) large items, c) diving next to a trawl net, d) picking off fish attached to outside of a trawl net, e) taking fish from inside a trawl net underwater, f) swimming upwards towards gear with a potential risk of entanglement, and scramble competition g) below the surface (gannets) and h) at the surface (gannets, lesser black-backed gulls *Larus fuscus* and northern fulmars *Fulmarus glacialis*).

4.4.3 Comparing scavenging and natural foraging

There was no significant difference between scavenging and natural foraging trips across nine measures of foraging effort (Figure 4.3, Table 4.2). There were also no sex differences in foraging effort (Table 4.2). Some measures of foraging effort were significantly higher in 2017 than in 2016 (dives per hour, trip duration, range, total distance and total ODBA), while others showed no year difference (speed, mean ODBA, time spent active and percentage of time spent active, Table 4.2). A similar pattern of foraging bouts consisting of repeated plunge dives occurred both during scavenging and natural foraging (Figure 4.4). When attending a vessel, gannets foraged with large numbers of conspecifics and large gulls (mainly lesser black-backed gulls *Larus fuscus*), as well as northern fulmars *Fulmarus glacialis* (Figure 4.2h). Scramble competition, where multiple individuals attempted to take the same item, was observed on multiple occasions (Figure 4.2g). This contrasted to natural foraging, during which gannets dived alone and alongside conspecifics, common dolphins *Delphinus delphis*, and Manx shearwaters *Puffinus puffinus* (Figure 4.5). We also observed black-legged kittiwakes *Rissa tridactyla* and European storm petrels *Hydrobates pelagicus* (Figure 4.5g) during scavenging and natural foraging events.

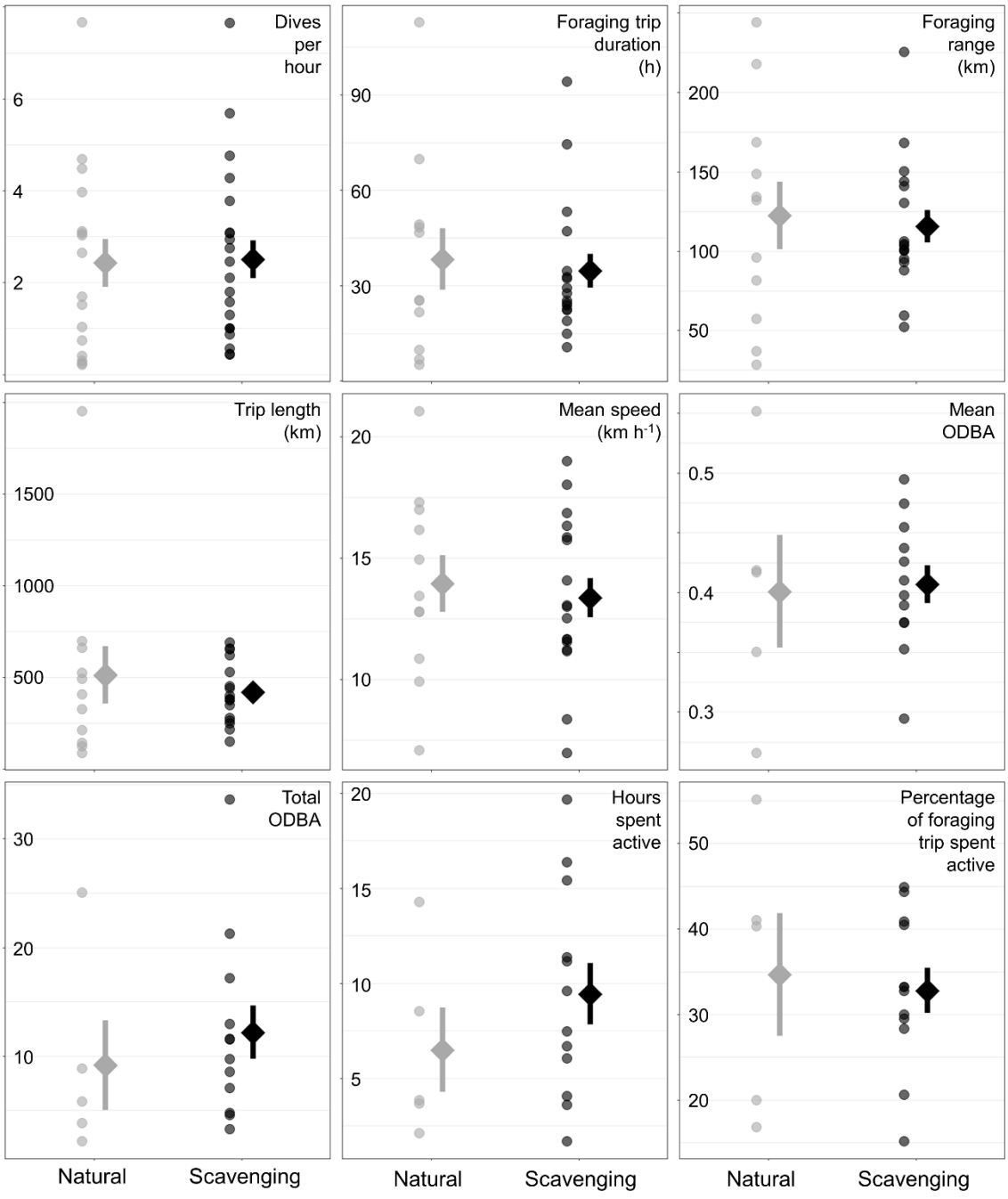


Figure 4.3. Comparison of foraging effort metrics for northern gannet *Morus bassanus* foraging trips between natural foraging (grey) and scavenging (black). Circles show metrics for individual trips and diamonds indicate the mean for each strategy ± standard error. There were no statistically significant differences to a level of $p < 0.05$ (Table 4.2). 'Active' = all behaviours apart from resting on the water.

Table 4.2. Metrics of foraging effort modelled in relation to scavenging, year and sex as categorical variables, with one trip for each individual. Statistically significant results to a level of $p<0.05$ are shown in **bold**. Estimates (est.) are shown ± standard error relating to the reference category (in parentheses). n = number of trips (scavenging trips (>50% dives at vessels), natural foraging trips). The full model was coded as: metric of effort ~ strategy + year + sex. The number shows the order in which variables were removed from the model (1 = first, 3 = last) using backwards stepwise deletion of the variable with the highest p value. 'Active' = all behaviours apart from resting on the water.

Metric	Foraging strategy (scavenging est. relative to natural foraging)	Year (2017 est. relative to 2016)	Sex (male est. relative to female)
Dives per hour n = 37 (21, 16)	1: est. = -0.136 ± 0.770, $\chi^2_{1,33} = 0.084$, p = 0.773	**3: est. = 1.638 ± 0.618,** **$\chi^2_{1,35} = 7.765$, p = 0.005**	2: est. = 0.782 ± 0.466, $\chi^2_{1,34} = 1.177$, p = 0.098
Trip duration (hours) n = 32 (17, 15)	2: est. = -3.581 ± 7.220, $\chi^2_{1,25} = 0.274$, p = 0.601	**3: est.= 23.74 ± 7.75,** **$\chi^2_{1,26} = 9.294$, p = 0.002**	1: est. = 3.486 ± 6.914, $\chi^2_{1,24} = 0.231$, p = 0.631
Foraging range (km) n = 32 (17, 15)	2: est. = -35.62 ± 18.62, $F_{2,25} = 3.662$, p = 0.067	**3: est. = 57.29 ± 17.91,** **$F_{1,26} = 10.239$, p = 0.004**	1: est. = 4.976 ± 17.017, $F_{3,24} = 0.086$, p = 0.772
Trip length (km) n = 32 (17, 15)	1: est. = -78.50 ± 87.93, $\chi^2_{1,24} = 0.883$, p = 0.347	**3: est. = 291.66 ± 100.43,** **$\chi^2_{1,26} = 8.302$, p = 0.004**	2: est. = 73.34 ± 88.65, $\chi^2_{1,25} = 0.658$, p = 0.417
Mean speed (km h^{-1}) n = 32 (17, 15)	1: est. = -0.389 ± 1.548, $F_{3,24} = 0.063$, p = 0.804	3: est. = -0.636 ± 1.370, $F_{1,26} = 0.216$, p = 0.646	2: est. = 0.605 ± 1.363, $F_{2,25} = 0.197$, p = 0.661
Mean ODBA n = 17 (12, 5)	2: est. = 0.034 ± 0.048, $F_{2,14} = 0.494$, p = 0.494	3: est. = -0.025 ± 0.036, $F_{1,15} = 0.465$, p = 0.506	1: est. = 0.005 ± 0.037, $F_{3,13} = 0.020$, p = 0.890
Total ODBA n = 17 (12, 5)	1: est. = 0.310 ± 3.234, $\chi^2_{3,13} = 0.000$, p = 1.000	**3: est. = 6.955 ± 3.270,** **$\chi^2_{1,15} = 4.124$, p = 0.042**	2: est. = 4.207 ± 3.129, $\chi^2_{2,14} = 1.830$, p = 0.176
Time active (mins) n = 17 (12, 5)	1: est. = 0.268 ± 2.211, $\chi^2_{3,13} = 0.018$, p = 0.894	2: est. = 3.519 ± 1.887, $\chi^2_{2,14} = 3.123$, p = 0.077	3: est. = 4.709 ± 2.591, $\chi^2_{1,15} = 3.555$, p = 0.059
Percent time active n = 17 (12, 5)	1: est. = -1.023 ± 3.268, $F_{3,13} = 0.098$, p = 0.759	2: est. = 4.324 ± 2.367, $F_{2,14} = 3.338$, p = 0.089	3: est. = 4.709 ± 2.434, $F_{1,15} = 3.743$, p = 0.072

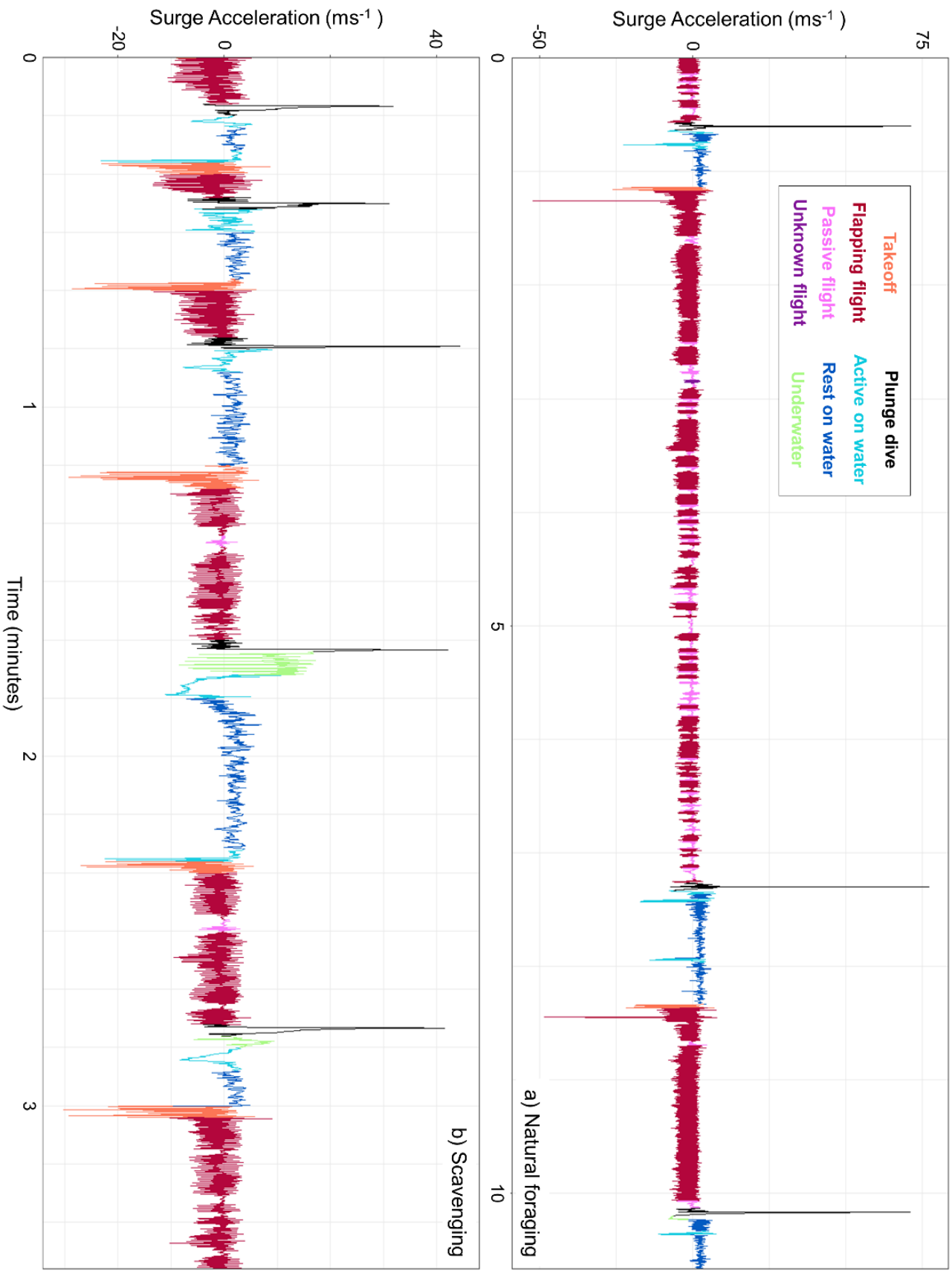


Figure 4.4. Example acceleration traces in the surge axis for series of northern gannet *Morus bassanus* plunge dives and takeoffs during foraging bouts for a) natural foraging and b) foraging at a vessel. Behaviours classified at two-second intervals using a video-validated random forest model with logic correction.

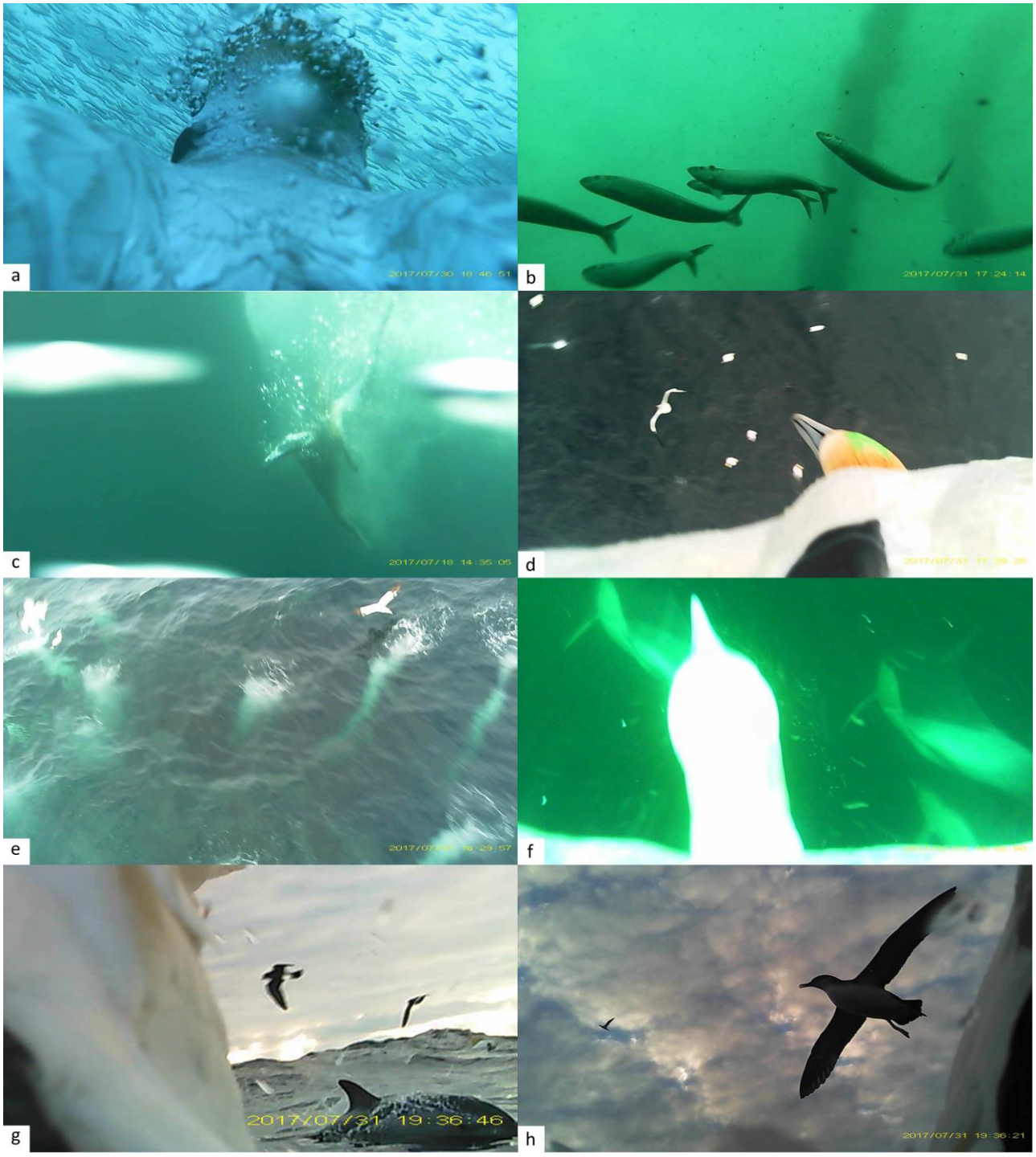


Figure 4.5. Example images from bird-borne video cameras showing natural foraging behaviour in northern gannets *Morus bassanus* from Grassholm, UK. Gannets hunting a) small fish and b) mackerel (bubble trails show previous routes of gannet dives), and with c) distant conspecifics that can be seen from d) the height of the plunge dive, along with e) their entry points and routes. Gannets foraging alongside other species including f) common dolphins *Delphinus delphis*, g) European storm petrels *Hydrobates pelagicus*, and h) Manx shearwaters *Puffinus puffinus*.

4.5 Discussion

In this study, we addressed several questions about how gannets use fishing vessels as a food source. We found that 59.5% of dives occurred at vessels. Scavenging was evenly distributed between the sexes or years of the study but was repeatable within individuals within a foraging trip. At vessels, gannets collected discards but also fed during trawl net hauling. There was no difference between scavenging and natural foraging in terms of effort, likely due to high levels of competition at vessels. We discuss our results in relation to the foraging decisions of individual gannets and the potential impacts of changes in fisheries practice or policy. We also highlight the benefits of combining bird-borne video cameras with GPS loggers and accelerometers to reveal aspects of ecology, behaviour and human-wildlife interactions in unprecedented detail.

4.5.1 Incidence of scavenging

We found a high incidence of scavenging among chick-rearing gannets, with 59.5% of dives occurring at vessels. This is consistent with previous studies showing that fisheries provide an important food source for breeding gannets in the Celtic Sea (Bodey *et al.,* 2014; Patrick *et al.,* 2015; Votier *et al.,* 2013). Moreover, scavenging was highly repeatable within foraging trips, with 17 birds diving only at vessels, 15 diving only naturally and five employing both strategies. This was not unexpected since breeding gannets are repeatable in other aspects of their foraging behaviour, such as location and search behaviour both within and between seasons (Patrick *et al.,* 2014; Votier *et al.,* 2017; Wakefield *et al.,* 2015), as well as in response to fishing vessels (Bodey *et al.,* 2018; Patrick *et al.,* 2015). Specialist scavengers that have become reliant on food subsidies may be vulnerable to changes in fisheries practice and policy (Oro *et al.,* 2013). Specifically, reforms of the EU Common Fisheries Policy are expected to reduce the fishery discards that subsidise the diets of scavenging species in Europe (Commission of European Communities, 2009). However, some birds foraged both naturally and at fishing vessels, revealing a degree of individual flexibility. Thus, this data provides a valuable baseline from which to evaluate the impacts of the discard ban on seabirds.

Overall, there were no sex differences in the likelihood of dives occurring at vessels (63.8% of females, 56.8% of males, Table 4.1). This is consistent with the finding that males and females from Grassholm did not differ in their selection

for areas of high fishing activity levels across eight years (Chapter 2). However, as in other similar studies, our small sample size makes it difficult to determine whether this is just sampling variation (Votier *et al.,* 2013). Although not statistically significant, we found a higher proportion of dives were at vessels in 2017 (64.8%) than in 2016 (47.1%, $X^2_1 = 3.044$, $p = 0.081$). In 2017, foraging effort was greater (Figure 4.3, Table 4.2), and colony productivity was lower than in 2016 (RSPB unpublished report, 2017), indicating that food availability may have been lower. These results are consistent with the interpretation that scavenging is more likely when food is scarce (Gilbert *et al.,* 2016; Hamer, Furness & Caldow, 1991; Monsarrat *et al.,* 2013; Tew Kai *et al.,* 2013; Votier *et al.,* 2004). This may relate to the lower nutritional quality of scavenged foods making them less desirable than natural prey, as recorded for Cape gannet *Morus capensis* (Grémillet *et al.,* 2008). As gannets ignore available fishing boats in some parts their range (Camphuysen, Heessen & Winter, 1995; Chapter 5), vessels may not be a favourable option unless natural prey is limited (Skov & Durinck, 2001).

4.5.2 Scavenging technique

We observed two main techniques of foraging at vessels: during discarding and during net hauling. Gannets fed on discards as they dropped from chutes (Figure 4.1a, 4.1b), both collecting items from the surface and plunge-diving. Most studies of seabird scavenging focus on discards, but we found that foraging from trawl nets was also common. We observed gannets picking bycaught fish from the outside of nets while underwater (Figure 4.1d) and taking fish through the mesh (Figure 4.1e). This technique may buffer scavenging specialists against the impacts of changes in discard availability. However, these resources may not be as available to surface-feeders, such as gulls, fulmars and storm petrels. Furthermore, individuals that dive around trawl nets came into close contact with loose ropes and netting that present an entanglement risk (Figure 4.1f; Croxall *et al.,* 2012; Lewison *et al.,* 2004). As such, continued research into seabird-fisheries interaction under different levels of discards availability would provide insight into the formation and maintenance of scavenging strategies, along with their associated risks.

4.5.3 Comparing scavenging and natural foraging

We found no difference in foraging effort between scavenging and natural foraging trips across any of the following metrics: dive frequency; foraging trip duration, range, total distance and mean speed; mean and total ODBA; and time and percentage of time spent active (Figure 4.3, Table 4.2). Moreover, the pattern of behaviours involved in foraging is broadly similar between scavenging and natural foraging bouts – i.e. most dives are not isolated but occur within a series of aerial plunge dives at the same vessel or prey patch, each requiring a costly takeoff (Figure 4.4). The depth of plunge dives may allow gannets to access fish sinking through the water column outside the reach of surface-feeding gulls and fulmars, and the speed of plunge dives may provide a competitive advantage in cases where multiple gannets attempt to take the same fish (Figure 4.2g). Scramble competition at vessels is intense, as considerable numbers of gannets and large gulls gather to scavenge (Figure 4.2g, 4.2h). As such, scavenging may have initially been an energetically favourable strategy, but vessels attracted more individuals to the point at which the energetic cost balances with that of natural foraging. Additionally, we observed gannets floating away from vessels after surfacing from a dive or landing on the water, and then later taking off and returning to the vessel. This could be due to the boat travelling faster than the gannet can efficiently swim, or it could be that gannets actively leave the area around the vessel to rest due to the very high density of conspecifics and other scavenging seabirds. While we observed multiple gannets underwater during natural foraging events, they were more distant (Figure 4.5), and we did not observe any antagonistic interactions (Figure 4.2). Scavenging also alters interspecific interactions; scavenging gannets spent more time with large gulls, which tend to be more aggressive. Conversely, natural foragers were more likely to either forage alone or with fewer and more distant conspecifics, along with common dolphins, European storm petrels, and Manx shearwaters (Figure 4.5).

Scavenging appears not to be an energy-saving strategy, requiring just as much effort as natural foraging, although we could not quantify energetic intake. Furthermore, scavenging seems to require a specific skill set that, while different from natural foraging, is similarly challenging. Scavengers must dive in very close proximity to competitors and often fail to gain food during a dive when another gannet reaches the same item first (Figure 4.2g). In contrast, natural foragers must capture live prey but rarely come into close contact with competitors during

dives (Figure 4.5c). This is likely to favour specialists that may become reliant of such predictable food sources. However, as scavenging involves a similar series of behaviours as natural foraging, scavengers may be able to adapt quickly to natural food sources. Given the risks of death or injury through bycatch and the potential lower nutritional quality of scavenged fish, scavenging may only be favourable when natural prey availability is low. This, coupled with the high incidence of scavenging, suggests that the loss of discards will negatively impact gannets in our study region. However, gannets may still be able to access some food from vessels during trawl net hauling.

4.5.4 Methodology

Methods used to study seabird-fisheries interactions include diet sampling (Bearhop *et al.,* 2001; Votier *et al.,* 2008), stable isotope analysis (Navarro *et al.,* 2009; Votier *et al.,* 2010), boat-based observations or experiments (Brothers, 1991; Maree *et al.,* 2014), and bio-logging techniques including matching bird-borne GPS with vessel density (Sommerfeld *et al.,* 2016; Chapter 2) or individual vessel tracks (Collet, Patrick & Weimerskirch, 2017a; Soriano-Redondo *et al.,* 2016; Chapter 5). Bio-logging is useful for attributing scavenging to birds from specific colonies and age classes (Votier *et al.,* 2013). In particular, cameras have the advantage of separating scavenging from situations where both birds and boats converge on the same prey hotspots. Cameras have also successfully detected underwater catch depredation, which can be harder to observe than discards collection (van den Hoff, Kilpatrick & Welsford, 2017). Cameras can also detect illegal, unreported and unregulated fisheries and small vessels that are not required to take part in vessel monitoring systems. However, they are less suitable for distinguishing birds ignoring vessels from a lack of available vessels (Cianchetti-Benedetti *et al.,* 2018; Sztukowski *et al.,* 2017), so simultaneously tracking birds and boats may be more appropriate for assessing this type of response (Chapter 5). Time-matched GPS and accelerometry data provide broad- and fine-scale information on foraging behaviour and effort that can be related to observed behaviours.

4.6 Conclusion

Here we provide one of the most detailed studies into the ecology of scavenging, by using combined deployments of bird-borne video cameras, GPS loggers and accelerometers. We show that fishing vessels provide an important food source for northern gannets in the Celtic Sea despite not providing energetic savings compared to natural foraging. As such fisheries subsidies may be most important when natural food availability is low. We find that scavenging is largely performed by a subset of specialists, which are likely to be impacted by a discard ban. However, scavengers also exploited vessels during net hauling above and below the surface, buffering discard losses but presenting a greater entanglement risk. With discard bans and other discard reduction measures becoming increasingly prevalent, we must consider the distribution of scavenging within populations and the specific behaviours involved when assessing the impacts of predictable anthropogenic food subsidies and changes to their availability.

Chapter 5 – Gannets are not attracted to fishing vessels in Iceland—potential influence of a discard ban and food availability

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5.1 Abstract

Fisheries produce large amounts of waste, providing food subsidies for scavengers. Discards influence seabird movement, demography and community structure, but little is known about seabird-fishery interactions where discarding is banned. Here we investigate how northern gannets Morus bassanus respond to fishing vessels in Iceland, where discarding commercial species is illegal, but birds may still access bait, offal or catch. We GPS-tracked 82 foraging trips for 36 breeding gannets from two colonies (Skrúður and Hellisey) and obtained time-matched vessel locations. We classified bird behaviour using Hidden Markov Models and then tested the effect of vessel distance on behavioural state-switching using multi-state Markov models. Fishing vessels were present during 94% of foraging trips. However, the likelihood of gannets switching from travelling to foraging was unaffected by vessel proximity, regardless of gear type or activity. When encountering vessels, gannets rarely foraged, but instead were more likely to continue travelling. As gannets scavenge from vessels in other regions, our findings suggest that discarding may be important in driving seabird-fishery interactions. When controlling for population size, gannet foraging trips at both colonies were shorter than expected, suggesting favourable conditions. The lack of behavioural responses to vessels among Icelandic gannets is likely driven by the discard ban and availability of pelagic fishes. Our findings have implications for understanding bycatch risk and the consequences of discard reforms.

Keywords: Predictable Anthropogenic Food Subsidies (PAFS); Vessel Monitoring Systems (VMS); behavioural response; Northern gannet; *Morus bassanus*; scavenging; seabird-fisheries interactions; biologging; GPS tracking; foraging

5.2 Introduction

Fisheries provide food subsidies in the form of discards, attracting large numbers of scavengers (Oro *et al.,* 2013). Seabirds are one of the most conspicuous consumers of fisheries waste (Sherley *et al.,* 2019), with at least 52% of seabird species eating discards (Oro *et al.,* 2013). While reducing discards is key for a sustainable fishing industry, this may considerably impact the large numbers of scavenging individuals (Bicknell *et al.,* 2013). On the other hand, many birds that feed at vessels are killed as bycatch (Lewison *et al.,* 2004), and reducing discarding may in turn reduce mortality. As a result, understanding the consequences of variation in discard availability is valuable for the study of marine ecology, as well as for ecosystem approaches to fisheries management (Zeller *et al.,* 2018).

Subsidies from fishing vessels affect seabird diet (Votier *et al.,* 2004), movement patterns (Bodey *et al.,* 2014), population dynamics (Oro *et al.,* 2004), species distributions (Arcos and Oro, 1996) and community composition (Church *et al.,* 2018). Seabird-fishery interactions are therefore important, yet complex. For instance, they vary among species (Collet *et al.,* 2017), populations (Petyt, 1995; Granadeiro *et al.,* 2011) and individuals (Votier *et al.,* 2010; Patrick *et al.,* 2015), with fishing vessels being a key resource in some regions while of little importance in others. For example, Scopoli's shearwaters *Calonectris diomedea* in the western Mediterranean follow fishing boats for food (Soriano-Redondo *et al.,* 2016), while most in the central Mediterranean do not (Cianchetti-Benedetti *et al.,* 2018). Similarly, in waters around New Zealand, White-capped albatrosses *Thalassarche steadi* overlap strongly with vessels (Torres *et al.,* 2011), while Campbell albatrosses *Thalassarche impavida* show limited attraction (Sztukowski *et al.,* 2017). The reasons for such variation in attraction to fishing vessels are not fully understood but may relate to differences in discard availability, naturally occurring foods, or both (Votier *et al.,* 2004).

Most research into fisheries interactions takes place in areas with high discarding rates, such as the UK (Votier *et al.,* 2013), the Mediterranean (Soriano-Redondo *et al.,* 2016) and the Benguela Current region (Tew Kai *et al.,* 2013). As such, comparing responses to fishing vessels in regions with differing discard availability could provide valuable insights into scavenging behaviour and the potential impacts of changing discarding practice. For

example, in Iceland, discarding is banned for all species of commercial value (Popsescu and Poulsen, 2012; Marchal *et al.,* 2016), and other measures have been introduced to reduce discarding, including increased trawl net mesh size (Sturludottir, 2018), transferable quotas (Woods *et al.,* 2015), a penalty-free allowance for landing undersized fish (Sturludottir, 2018), and real-time closures in response to undersized fish (Björnsson *et al.,* 2015). Illegal discarding occurs despite these measures, but estimated rates are low at 0.9% for cod *Gadus morhua* and 2% for haddock *Melanogrammus aeglefinus* (Valtýsson, 2014), compared to 8-22% for haddock in the late 20th century (Sturludottir, 2018). While there are no other species-specific estimates of discard rates for Iceland, overall discard rates were estimated at 2.8% in 2010 (Valtýsson, 2014; Zeller *et al.,* 2018). The fate of discards in Iceland is also unknown, aside from records of discard consumption by northern fulmar *Fulmarus glacialis* (Lilliendahl and Solmundsson, 1997; Sturludottir, 2018). Offal dumping, where waste from gutting marketable catch is disposed of, is permitted but has not been quantified (Guðjón Már Sigurðsson, pers. comm.). Overall, discards are not widely available to birds in Icelandic waters, but there is little known about seabird-fishery interactions there.

Northern gannets *Morus bassanus* are a regular scavenger in some parts of their range (Votier *et al.,* 2010, 2013), but their interactions with fishing boats have not been studied in Icelandic waters. Gannets vary regionally in scavenging tendency, with strong responses to vessels in the Celtic sea (Bodey *et al.,* 2014; Patrick *et al.,* 2015), where discarding rates are high, but limited attraction in the North Sea (Camphuysen, Heessen & Winter, 1995). There may also be seasonal differences in discard use in some regions, with more gannets observed feeding on discards in the North Sea in winter than in summer (Camphuysen *et al.,* 1995). This spatial and temporal variation in scavenging behaviour is poorly explained and may be related to variation in the availability of discards and alternative foods.

As well as discards, fisheries present other foraging opportunities. Offal may available in Iceland, but gannets rarely feed on this, instead preferring discarded whole fish, particularly gadoids (Camphuysen *et al.,* 1995). Gannets may also take bait or catch from longlines (García Barcelona *et al.,* 2010), while fish corralled into nets provide a focal point for diving (Petyt, 1995). These behaviours bring gannets in contact with fishing gear, with the potential for

injury and death, particularly for those attending longliners (Oliveira *et al.,* 2015). At trawlers, collision with warp cables and entanglement are risks (Watkins *et al.,* 2008). Bycatch data for gannets in Iceland is limited to gillnets (Anderson *et al.,* 2011), with few caught, but elsewhere in their range where discarding is common (Portugal, Canada and the USA), gannets experience high bycatch from gillnets, longlines, trawls and seines (Žydelis *et al.,* 2013; Oliveira *et al.,* 2015). As seabird mortality risk at vessels is increased by discarding or dumping offal while gear is still in the water (Pierre *et al.,* 2010; Maree *et al.,* 2014), understanding the role of discarding in attracting gannets to vessels could help to explain the regional variation in gannet bycatch rates.

To investigate whether gannets are attracted to forage at fishing vessels in a region where discarding is banned, we GPS-tracked chick-rearing adults at two Icelandic colonies. Here we used Hidden Markov Models to classify gannet behaviour and then investigated the influence of vessel proximity on changes between these behavioural states using multi-state Markov models. We also examined responses to different gear types with differing levels of potential foraging opportunities during hauling or due to variation in potential spillage of fish or illegal discarding. We also calculated foraging trip duration, range and distance travelled as measures of foraging effort and compared this against estimates from other gannet colonies to indicate natural food availability.

5.3 Methods

5.3.1 Study sites and sampling

GPS-tracking took place in July 2016 and 2017 at two colonies in Iceland: Skrúður (64.900ºN, 13.632ºW) and Hellisey (63.361ºN, 20.366ºW). Skrúður had 6,051 apparently occupied nests (AONs) in 2013. Hellisey had 3,374 AONs in 2014 but is part of the Vestmannaeyjar archipelago, which had 15,044 AONs in 2013/14 (Garðarsson, 2019). We captured chick-rearing gannets at the nest using a pole and noose and attached Mobile Action Technology ‘i-gotU’ GPS loggers to the central tail feathers with Tesa® tape. We deployed 48 loggers and retrieved 38 after one to three days. Two loggers failed, yielding 36 datasets with GPS locations every minute (Skrúður 2016-17 and Hellisey 2017) or two minutes (Hellisey 2016). GPS loggers weighed 20g (i-gotU 120) or 35g (i-gotU 600), which were 0.7% or 1.2% of the lightest bird. In 2016, ten birds were equipped with i-gotU 120 GPS loggers, accelerometers (Gulf Coast Data

Concepts X16-mini) and altimeters (MSR-145W), totalling 54g (1.9% of the lightest bird). The acceleration and altitude data are not used in this study. Previous studies found no effects of similar loggers on foraging trip duration or body mass for chick-rearing gannets (Hamer *et al.,* 2000). We collected diet samples for tracked adults that spontaneously regurgitated food, and chick diet was surveyed concurrently during annual ringing. Protocols were completed with the permission of the Icelandic Institute of Natural History with ethical approval from the University of Exeter (2016/1519). We extracted foraging trips from bird-borne GPS loggers when birds exceed 2km from the colony using the 'raster' (Hijmans, 2018) R package.

5.3.2 Gannet foraging trips

We removed trips of one GPS fix, partial trips (no return within 2km of the nest), and trips of less than 5km from the colony to account for rafting (Bodey *et al.,* 2014). We calculated the foraging trip duration, the foraging range as the maximum distance reached from the colony, and the total distance as the summed distance between each successive GPS location. We then compared trip duration, as a proxy for food availability, in relation to the square-root of colony size with the data for other colonies published in Lewis *et al.* (2001).

5.3.3 Co-occurrence of gannets and fishing vessels

To assess co-occurrence with tracked gannets, we used time-matched fishing vessel locations and vessel speeds at approximately 10-minute frequency. We obtained vessel locations from the Icelandic Directorate of Fisheries recorded by either satellite-based Vessel Monitoring Systems (VMS) or radio-based Automatic Identification Systems (AIS) for fishing vessels of all sizes (Geirsson, 2011). This covered the two study periods (29/6/16 to 12/7/16 and 29/6/17 to 12/7/17) across the gannet foraging areas for Skrúður (64ºN to 66ºN, 15.5ºW to 11.5ºW) and Hellisey (62.5ºN to 64ºN, 23.1ºW to 19ºW). We excluded records for which a vessel ID could not be obtained (approximately 7% of records), with 245,731 vessel locations remaining for analysis. Gear type was obtained for 77% of vessels by cross-referencing with the Icelandic Directorate of Fisheries Logbook database (Geirsson, 2011). For 4% of records, the gear type was known for one day, but unknown for the previous or next day and the vessel remained within the study area for a 30-minute window around midnight, so we

relabelled these records with the previous or next gear type. We classified vessel activity as “steaming”, “drifting” and “fishing” using gear-specific speed thresholds (Supplementary Table 1; Gerritsen and Lordan, 2011; Bodey *et al.,* 2014).

For each trip, we recorded the presence of vessels and vessels travelling at fishing speed within the foraging range during the trip duration. We classified bird behaviour into “travelling”, “resting” and “foraging” states based on step length and turning angle with a three-state Hidden Markov Model implemented using the ‘moveHMM’ R package (Michelot *et al.,* 2016), using linear interpolation to regularise the GPS data to sampling frequency (one or two minutes). Distributions of step length and turning angle for each state, and model checks were typical for the method (Supplementary Figures 1-3), which has been tested for northern gannet foraging behaviour using dive loggers to ground-truth foraging behaviour (Bennison *et al.,* 2017). Hidden Markov Models proved more successful than k-Means clustering, first passage time, speed/tortuosity thresholds, kernel density, effective maximization binary clustering and machine learning (Bennison *et al.,* 2017). We recorded the instances of each behaviour occurring within 1km, 2km and 11km of the nearest vessel; 1km and 2km indicate potential scavenging, and gannets respond to vessels at 11km away (Bodey *et al.,* 2014). These distance categories are not mutually exclusive, such that if a vessel is within 1km, it is also within 2km.

5.3.4 Behavioural response to fishing vessels

To quantify behavioural responses to nearby vessels, we investigated the effect of vessel distance on the probability of switching from travelling to foraging behaviour (See Figure 5.1 for the modelling process). We choose to model the probability of switching to foraging rather than the probability of foraging because this is more likely to represent a direct response to the vessel. On the other hand, if a bird is already foraging while a vessel approaches (perhaps even using the foraging gannets as a cue for locating fish), the foraging behaviour may be unrelated to the proximity of the vessel.

We used the behavioural classifications from the Hidden Markov Models detailed above to identify instances where gannets switched between the behavioural states of travel, foraging and rest. We then modelled state-switching probability using multi-state Markov models implemented in the ‘msm’

R package (Jackson, 2011; Bodey *et al.,* 2014). We did not use more recently developed packages, as these interpolate covariates where data are unavailable, which is inappropriate for distance to the nearest vessel. We extracted the location of each vessel before and after each regularised bird location, and linearly interpolated vessel tracks to the time of the bird record. We calculated distances to the nearest: 1) vessel, 2) trawler (Danish seine, pelagic trawl, otter trawl and Nephrops trawl) that may provide scavenging opportunities during net hauling, 3) demersal trawler (Nephrops and otter trawls) that have high historical discard rates indicating a higher probability of illegal discarding, and 4) vessel travelling at fishing speed, as intermediate speeds may reflect hauling or sorting and so relate to higher potential food availability for scavenging seabirds. We modelled state (travel, forage or rest) in relation to time, with the distance to the nearest vessel, trawler, demersal trawler and vessel travelling at fishing speed fitted as a binary covariate for each 1km interval up to 25km (Bodey *et al.,* 2014).

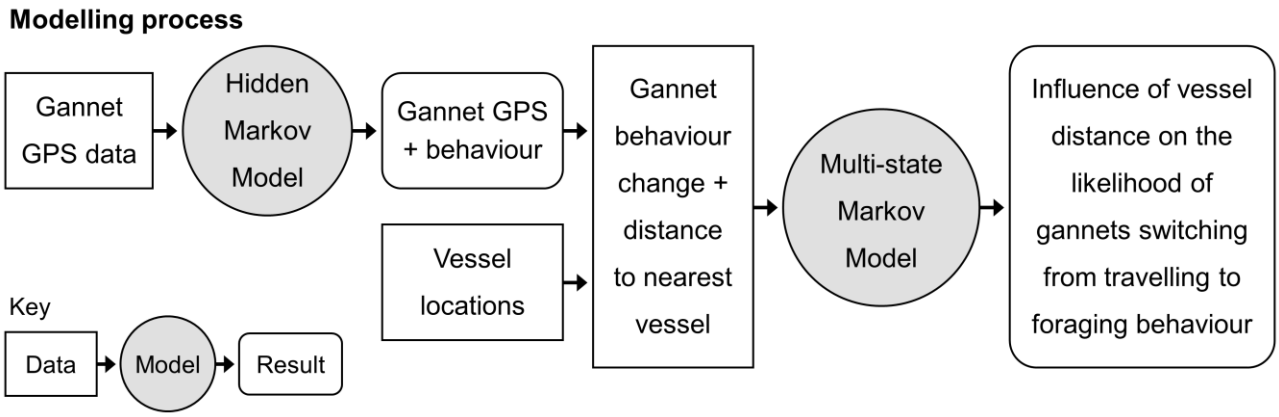


Figure 5.1. An outline of the two-stage modelling process for investigating the influence of fishing vessel proximity on northern gannet *Morus bassanus* foraging behaviour.

5.4 Results

5.4.1 Gannet foraging trips

We recorded 82 complete foraging trips for 36 individuals (Figure 5.2)—30 trips for nine birds from Hellisey, and 52 trips for 27 birds from Skrúður. For Hellisey and Skrúður respectively, the mean ± standard deviation trip durations were 10.23 ± 7.41 and 4.81 ± 4.53 hours, foraging ranges were 42.95 ± 27.04 and 29.19 ± 24.16 km from the colony, and total distances travelled were 150.16 ± 127.93 and 93.55 ± 85.52 km. The mean foraging trip durations for each colony were lower than expected for the colony size, particularly for Skrúður (Figure 5.3).

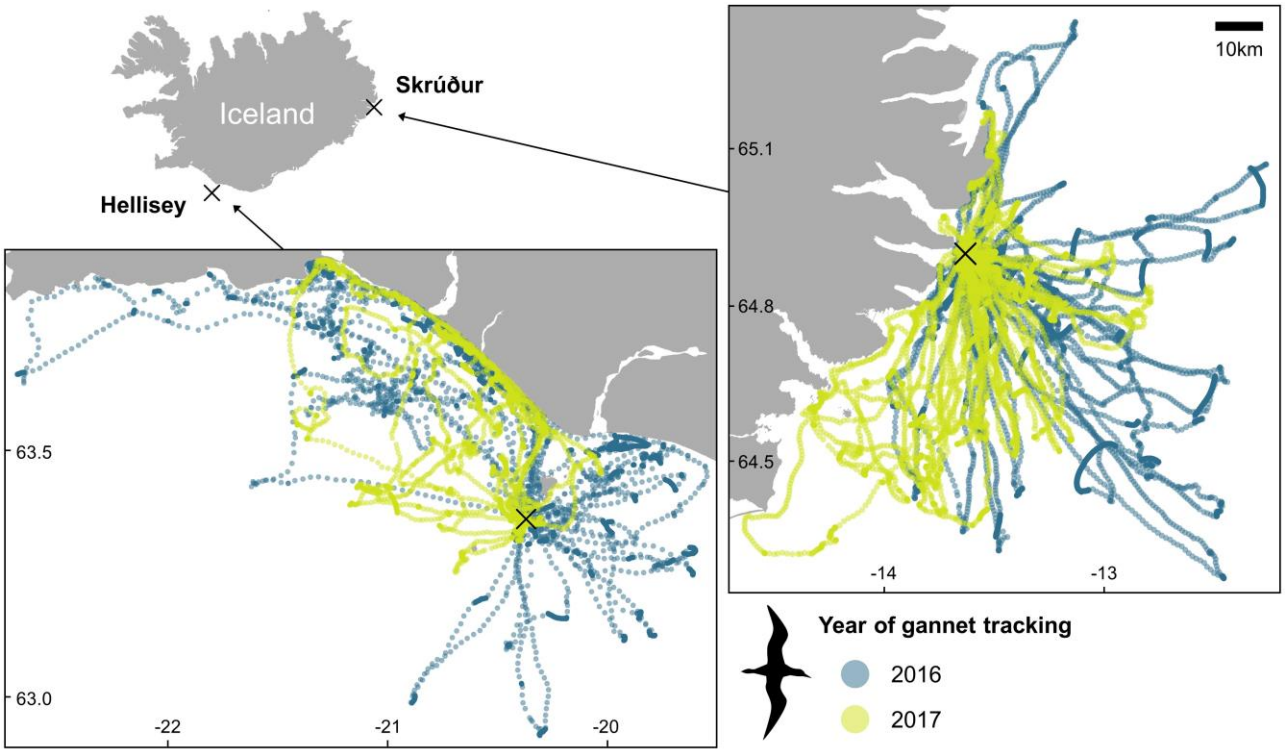


Figure 5.2. Foraging trips for chick-rearing northern gannets *Morus bassanus*, from Hellisey and Skrúður, Iceland, coloured by sampling year. Map adapted from tiles by Stamen Design, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

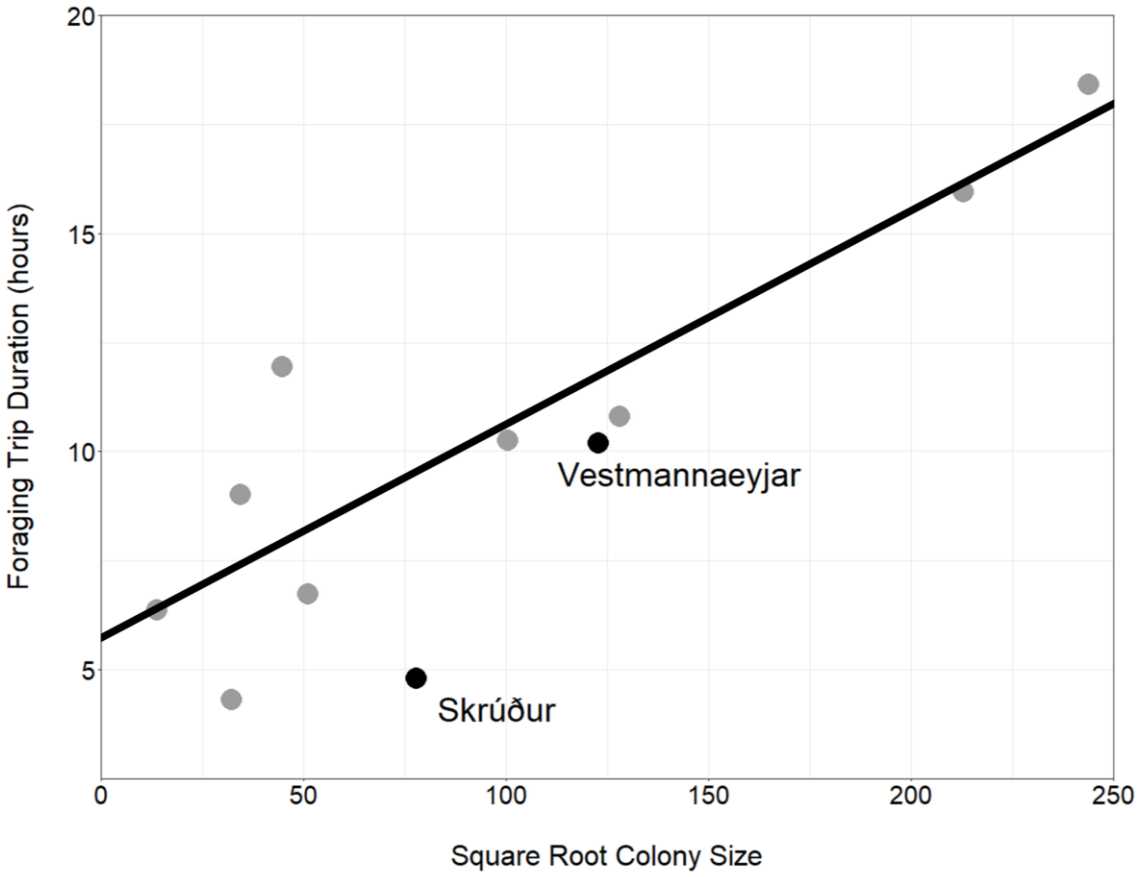


Figure 5.3. Mean foraging trip durations for northern gannet *Morus bassanus* colonies in relation to the square root of colony size. Grey circles indicate trip durations from Lewis *et al.* (2001), and the black line shows a linear relationship for just these nine colonies observed in 2000. Black circles indicate the colonies in this study.

5.4.2 Co-occurrence of gannets and fishing vessels

Fishing vessels were present in the spatial and temporal range of 94% of gannet foraging trips (n = 77) and were travelling at fishing speeds for 76% of the trips (n = 62). The nearest vessel to each gannet location used mainly handlines or longlines, but 24% of the nearest vessels were trawlers (Table 5.1). Hidden Markov Models assigned behaviours to all 33,323 regularised bird locations, with 27% labelled as foraging. Gannets rarely foraged close to vessels, with only 1.9% of foraging locations occurring within 1km of a vessel, despite 38% occurring within 11km (Table 5.2). Visual inspection of the tracks coded by behaviour and by time confirmed that gannets generally continued travelling when encountering a vessel (Figure 5.4).

Table 5.1. Number of vessel records within the study area encompassing the foraging ranges for each colony (Skruður: 64–66ºN, 15.5–11.5ºW and Hellisey: 62.5–64ºN, 23.1–19ºW) and time window during which gannets were tracked (29 June 2016 to 12 July 2016 and 29 June 2017 to 12 July 2017) with each gear type or category, and the number of regularized northern gannet *Morus bassanus* locations where the nearest vessel at the time has that gear type or category.

		Vessel records		Gannet locations	
Category	Gear Types	Number of vessel records	Percentage	Nearest vessel gear type	Percentage
Total	All gears	245,731	100 %	33,323	100 %
Single gear	Longline	39,007	15.9 %	9,514	28.6 %
	Gillnet	1,319	0.5 %	0	0 %
	Handline	119,411	48.6 %	9,744	29.2 %
	Danish Seine	6,618	2.7 %	2,475	7.4 %
	Otter trawl	13,375	5.4 %	2,179	6.5 %
	Pelagic trawl	12,238	5.0 %	2,562	7.7 %
	Nephrops trawl	6,975	2.8 %	902	2.7 %
	Unknown	46,788	19.0 %	5,947	17.8 %
Trawler	Danish seine, pelagic/otter/ Nephrops trawl	39,206	16.0 %	8,118	24.4 %
Demersal trawlers	Otter trawl, Nephrops trawl	20,350	8.3 %	3,081	9.2 %
Fishing speed	All gear types	113,308	46.1 %	12,333	37.0 %

Table 5.2. Number of northern gannet *Morus bassanus* locations for each behaviour occurring within specified distances of the nearest fishing vessel.

		Distance to vessel		
Behaviour	Total	< 11km	< 2km	< 1km
All	33,323	12,797 (38%)	1,150 (3.5%)	472 (1.4%)
Foraging	9,029	3,444 (38%)	337 (3.7%)	175 (1.9%)
Resting	15,635	5,426 (35%)	547 (6.3%)	227 (2.6%)
Travelling	8,659	3,927 (45%)	266 (1.7%)	70 (0.4%)

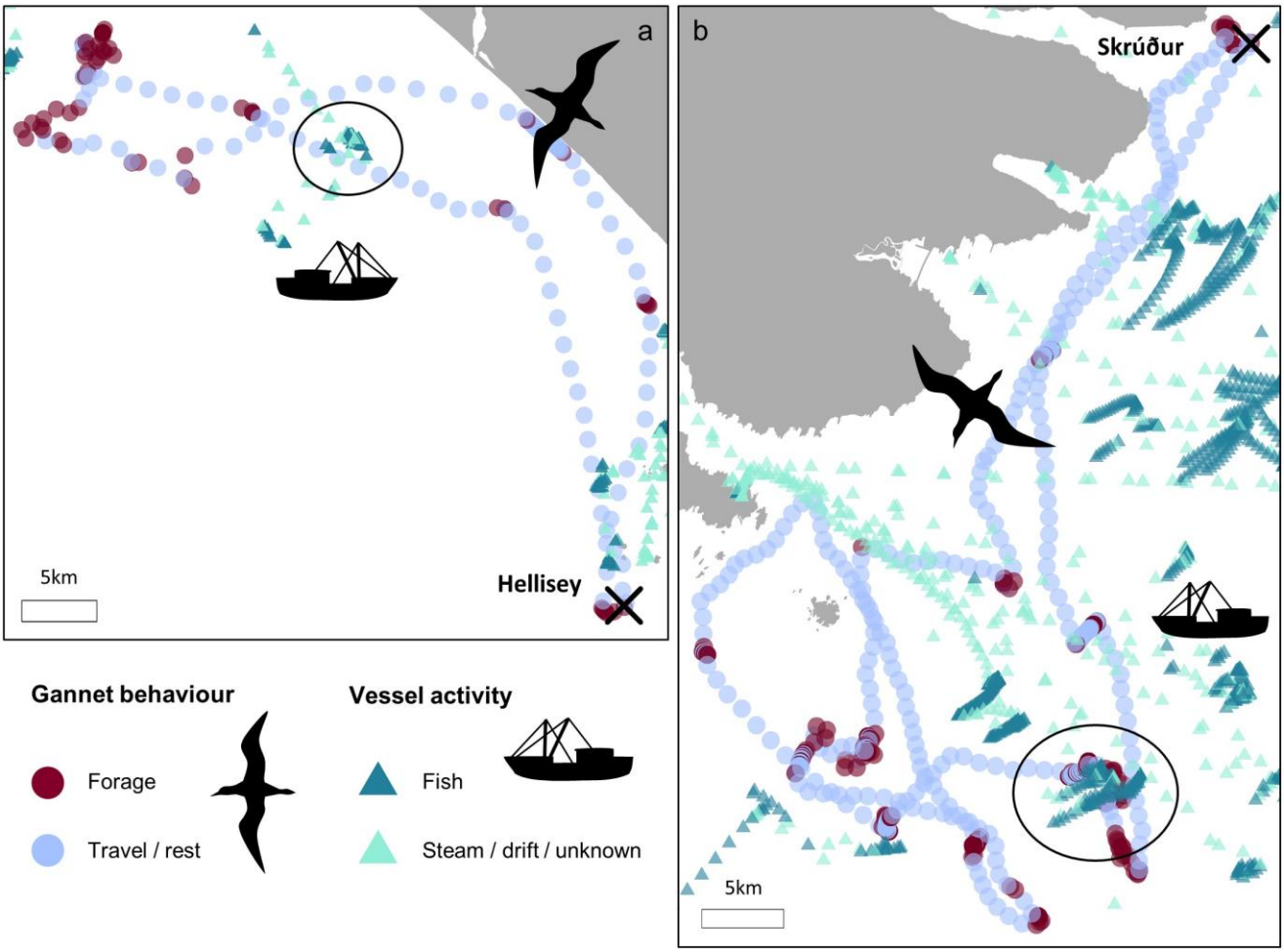


Figure 5.4. Examples of one foraging trip for a northern gannet *Morus bassanus* from a) Hellisey and b) Skrúður with regularised GPS locations coloured by behaviours (circles), and fishing vessel locations from the duration of the foraging trip coloured by activity (triangles). Black ovals show the gannet is near to vessels in space and time. In a), the bird travels past a vessel travelling at fishing speed without switching behaviour. In b), the bird forages within 1km of a vessel, which occurred rarely (<2% of gannet foraging locations). Map adapted from Stamen Design tiles, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

5.4.3 Behavioural response to fishing vessels

We recorded 691 transitions from travelling to foraging states. Multi-state Markov models show no significant effect of the distance to the nearest vessel, demersal trawler or vessel travelling at fishing speed on gannets switching from travelling to foraging. Gannets were slightly more likely to switch to foraging within 4km of the nearest trawler, but we did not detect an effect for any other distance (Figure 5.3; Table S5.2).

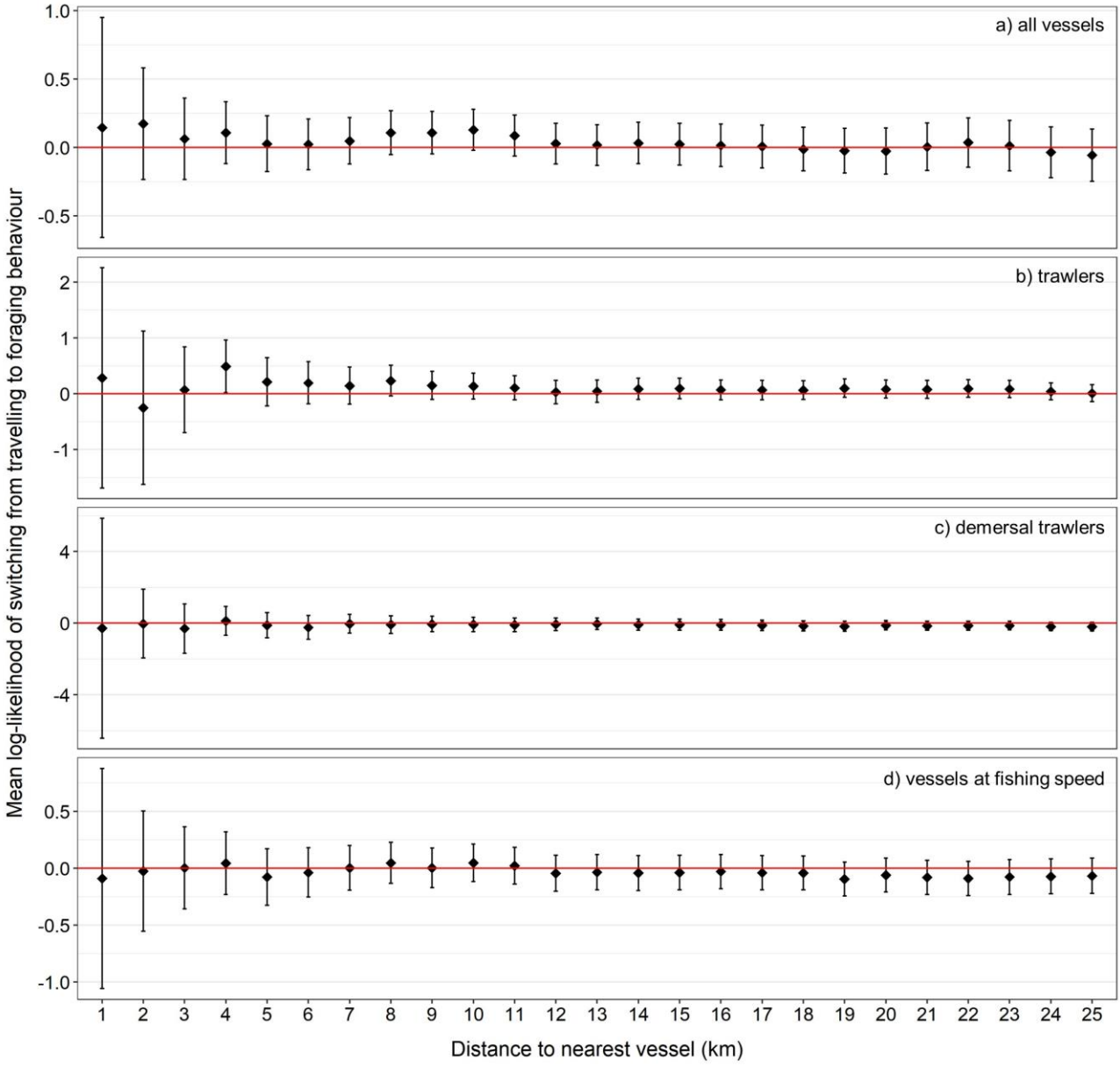


Figure 5.3. Mean log-likelihood of northern gannets *Morus bassanus* switching from travelling to foraging behaviour (+/- 95% Confidence Intervals (CIs)) in relation to different distances to the nearest: a) vessel, b) trawler (otter/Nephrops/pelagic/Danish seine), c) demersal trawler (otter/Nephrops), and d) vessel travelling at fishing speed. CIs crossing 0 (red line) indicate that the covariate does not have a significant effect.

5.4.4 Diet

We examined regurgitates from three tracked adults, all of which contained mackerel *Scomber scombrus.* Concurrent sampling of 159 chick regurgitates from Hellisey and Skrúður for 2016 and 2017 revealed 49.4% herring *Clupea harengus*, 44.4% mackerel, 2.5% Capelin *Mallotus villosus* or similar, 1.2% gadoid and 2.5% unidentified fish (Table S5.3).

5.5 Discussion

We investigated interactions between foraging gannets and fisheries in Icelandic waters, where discarding is banned. Fishing vessels were abundant within the gannets' foraging range, but there was little evidence of attraction to vessels—the distance to the nearest vessel did not influence the probability of gannets switching from travelling to foraging, regardless of gear type and fishing activity. Gannet diet samples were dominated by naturally occurring pelagic fishes, and short trip durations implied this prey was plentiful. The potential reasons for gannets ignoring fishing vessels in Iceland, and the wider implications of this behaviour, are discussed below.

5.5.1 Variation in behavioural response to fishing vessels

Icelandic gannets largely ignore vessels even though fish are available during net hauling (Petyt, 1995). Our findings contrast with the strong behavioural response of gannets to fishing activity in the Celtic Sea where discarding is common (Votier *et al.,* 2013, 2010; Bodey *et al.,* 2014; Patrick *et al.,* 2015). Bodey *et al.* (2014) found that gannets were more likely to switch from travelling to foraging when closer to a vessel and the response was stronger for vessels travelling at fishing or catch sorting speed. This comparison contributes to a growing literature showing that attraction to vessels varies not only among species (Collet, Patrick & Weimerskirch, 2017b) but also within species in different regions (Soriano-Redondo *et al.,* 2016; Cianchetti-Benedetti *et al.,* 2018). Such differences likely relate to variation in discard rates. For instance, long-term variation in discard consumption by great skuas *Stercorarius skua* is closely correlated with changes in discard rates (Votier *et al.,* 2004; Church *et al.,* 2018). Moreover, seabird bycatch rates can be higher during discarding and offal dumping (Watkins *et al.,* 2008; Pierre *et al.,* 2010; Maree *et al.,* 2014). This evidence suggests that discarding is important in determining the extent to which seabirds are attracted to fishing vessels (Wahl and Heinemann, 1979).

Food availability may also contribute to regional variation in seabird-fisheries interactions. Scavenging is less likely when natural food is plentiful (Hamer *et al.,* 1991; Skov and Durinck, 2001; Tew Kai *et al.,* 2013; Church *et al.,* 2018), partly because scavenged foods can have lower nutritional quality compared to natural prey (Grémillet *et al.,* 2008). Conditions in Iceland seem to be favourable for gannets—there is likely to be ample natural prey, as

evidenced by shorter foraging trips than expected given the respective sizes of the two colonies studied here (Figure 5.3). Recent influxes of pelagic fish linked to climate warming (Vigfúsdóttir *et al.,* 2009; Astthorsson *et al.,* 2015), and a relatively small gannet population compared to the Celtic Sea may have resulted in little competition for resources (Murray *et al.,* 2015; Garðarsson, 2019). We found that most gannet diet samples were pelagic fishes (94% herring or mackerel, consistent with surveys of gannet chick diet in 2006, 2007, 2011 and 2013; Vigfúsdóttir *et al.,* 2009; Vigfúsdóttir, unpubl. data). These species are the subject of commercial fisheries but are also available as natural caught prey. Therefore, while the evidence is only circumstantial, Icelandic gannets may be ignoring fishing vessels because pelagic prey is plentiful.

5.5.2 Implications for impacts of discard bans

Discard bans are being introduced in the European Union, Norway, Chile and New Zealand to improve the sustainability of the fishing industry (Marchal *et al.,* 2016). Our results suggest that in areas with low discard rates and apparently sufficient natural prey, seabird scavenging is likely to be limited, and so populations may be little affected. However, we can be less certain of the response of seabirds to discard bans in waters with historically high discard rates, where they may have become dependent on subsidies (Oro *et al.,* 1995; Bicknell *et al.,* 2013; Sherley *et al.,* 2019). Gannets show repeatable responses to fisheries (Votier *et al.,* 2010; Patrick *et al.,* 2015; Bodey *et al.,* 2018), and such individual behaviours are likely to be learned (Votier *et al.,* 2017). Gannets and other seabirds also use social information and follow conspecifics to prey patches (Weimerskirch *et al.,* 2010; Thiebault *et al.,* 2014; Jones *et al.,* 2018), with large aggregations often forming at fishing vessels (Wahl and Heinemann, 1979; Camphuysen *et al.,* 1995). This combination of individual learning and social information is likely to enhance regional variation in attraction to vessels by encouraging individuals to become specialist scavengers. Our findings also highlight the importance of maintaining healthy stocks of alternative foods for scavenging species, which may be able to switch back to a more natural diet in the face of discard bans (Bicknell *et al.,* 2013).

5.5.3 Implications for bycatch

Fishing gear kills very large numbers of seabirds (Anderson *et al.,* 2011; Lewison *et al.,* 2004), yet factors influencing bycatch rates are not fully understood. However, variation in discarding is likely to be important. Boat-based studies reveal increased bycatch during discarding or offal dumping (Watkins *et al.,* 2008; Maree *et al.,* 2014) and bycatch reductions when discarding is delayed until gear is out of the water (Pierre *et al.,* 2010). Gannets are consistently bycaught by fisheries in the north Atlantic (Žydelis *et al.,* 2013; Oliveira *et al.,* 2015; García Barcelona *et al.,* 2010), although they are rarely recorded as bycatch in Icelandic waters (Anderson *et al.,* 2011). An assessment of seabird bycatch in relation to spatial and temporal variation in rates of discarding would provide much-needed information on the risks of fisheries management to seabirds.

5.5.4 Methods for assessing seabird-fishery interactions

Simultaneously tracking seabirds and fishing vessels has provided important insights into seabird-fisheries interactions (Votier *et al.,* 2010; Granadeiro *et al.,* 2011; Soriano-Redondo *et al.,* 2016; Collet, Patrick & Weimerskirch, 2017b; Sztukowski *et al.,* 2017; Cianchetti-Benedetti *et al.,* 2018). This approach has some advantages over boat-based observations (Watkins *et al.,* 2008) that cannot determine the origin and status of seabirds that follow vessels or the repeatability of their behaviours, and dietary analysis (Votier *et al.,* 2004) that cannot always distinguish between scavenged and natural prey, and does not provide information about the availability of vessels. Crucially, neither method can provide information on birds that ignore all available fishing vessels. However, tracking may fail to establish whether interactions represent scavenging, or fishers and birds targeting the same prey. To achieve this requires more detailed information such as from bird-borne cameras (Votier *et al.,* 2013) or very high-resolution tracking. Moreover, VMS and AIS used to track vessel movements may be limited to large vessels. This was not a concern in Iceland because locations were available for all vessel sizes. Studying seabird-fishery interactions is best understood using a range of different approaches.

5.6 Conclusion

To conclude, we show that, despite foraging in waters with abundant fishing activity, Icelandic gannets did not respond to nearby vessels. This is likely explained by the low levels of discarding from these vessels and high availability of natural foods. We therefore believe it is important to consider regional variation in behaviour, particularly when predicting bycatch mortality and the impacts of large-scale changes in fisheries practice or policy.

5.7 Supplementary material

Table S5.1 shows gear-specific speed thresholds used to classify vessel activity. Figures S5.1, S5.2 and S5.3 show histograms and residuals for the Hidden Markov Models used to classify bird behaviour. Table S5.2 gives the estimates and confidence intervals plotted in Figure 5.5. Table S5.3 provides a breakdown of diet samples by colony, year and age class.

Table S5.1. Gear-specific minimum and maximum fishing speeds based on those provided in Bodey *et al.,* 2014.

Gear type	Minimum fishing speed (knots)	Maximum fishing speed (knots)
Longline or handline	0.1	4.5
Danish seine	0.5	4.5
Pelagic trawl	0.5	6.0
Nephrops or otter trawl	0.5	5.5
Gear unknown	0.5	4.5

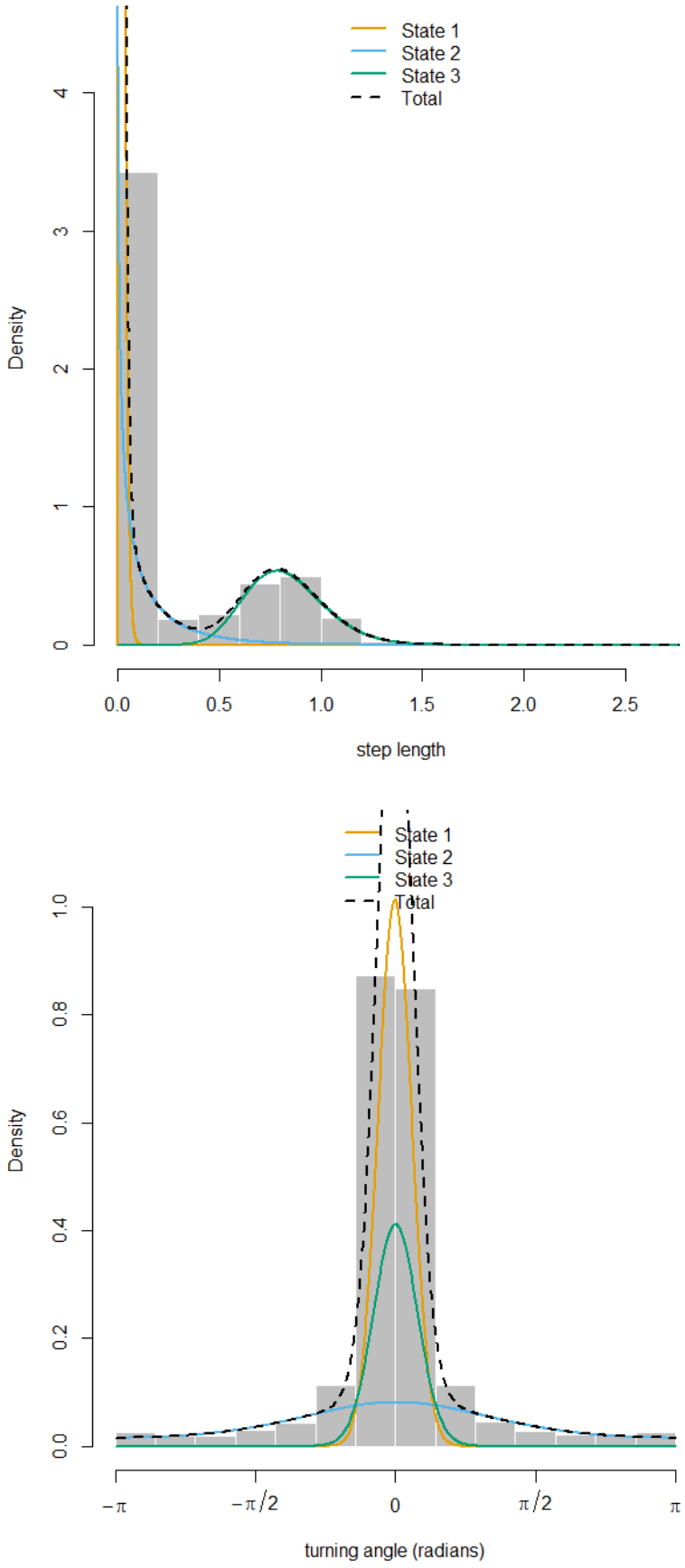


Figure S5.1. Histograms and densities for step length and turning angle for the Hidden Markov Model using to differentiate “resting” (State 1 - orange), “foraging” (State 2 - blue) and “travelling” (State 3 - green) in northern gannets *Morus bassanus.*

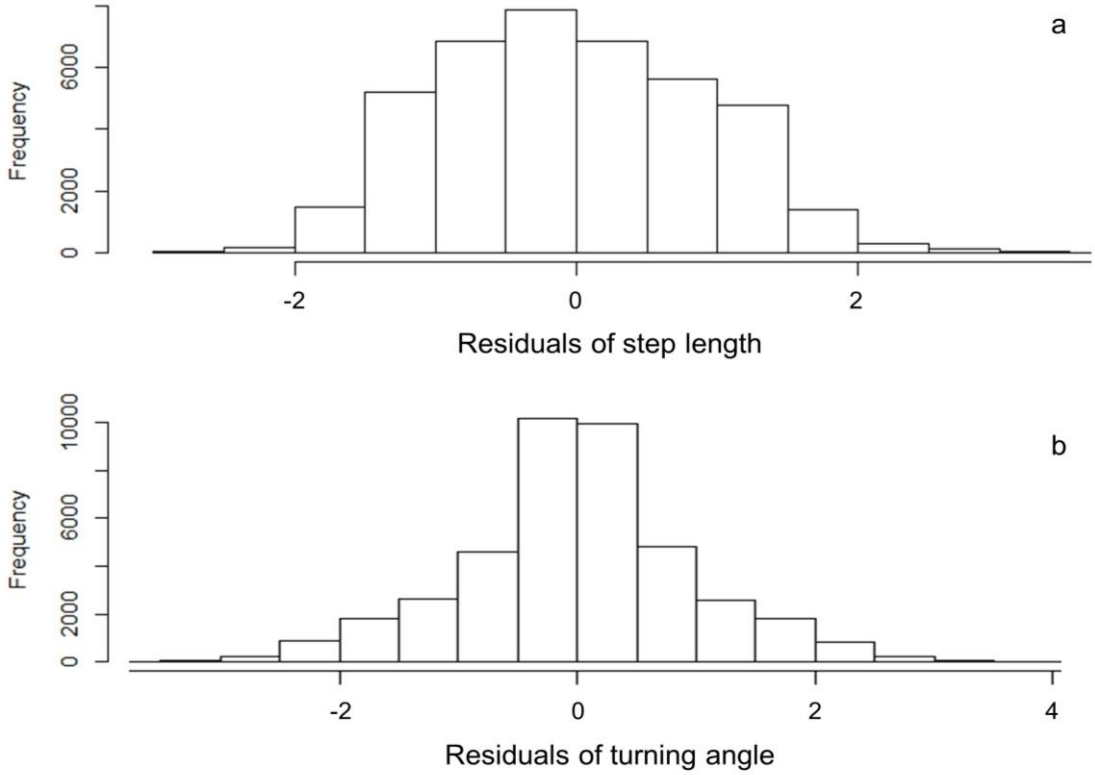


Figure S5.2. Histogram of residuals for a) step length and b) turning angle for the Hidden Markov Model used to differentiate “resting”, “foraging” and “travelling” in northern gannets *Morus bassanus.*

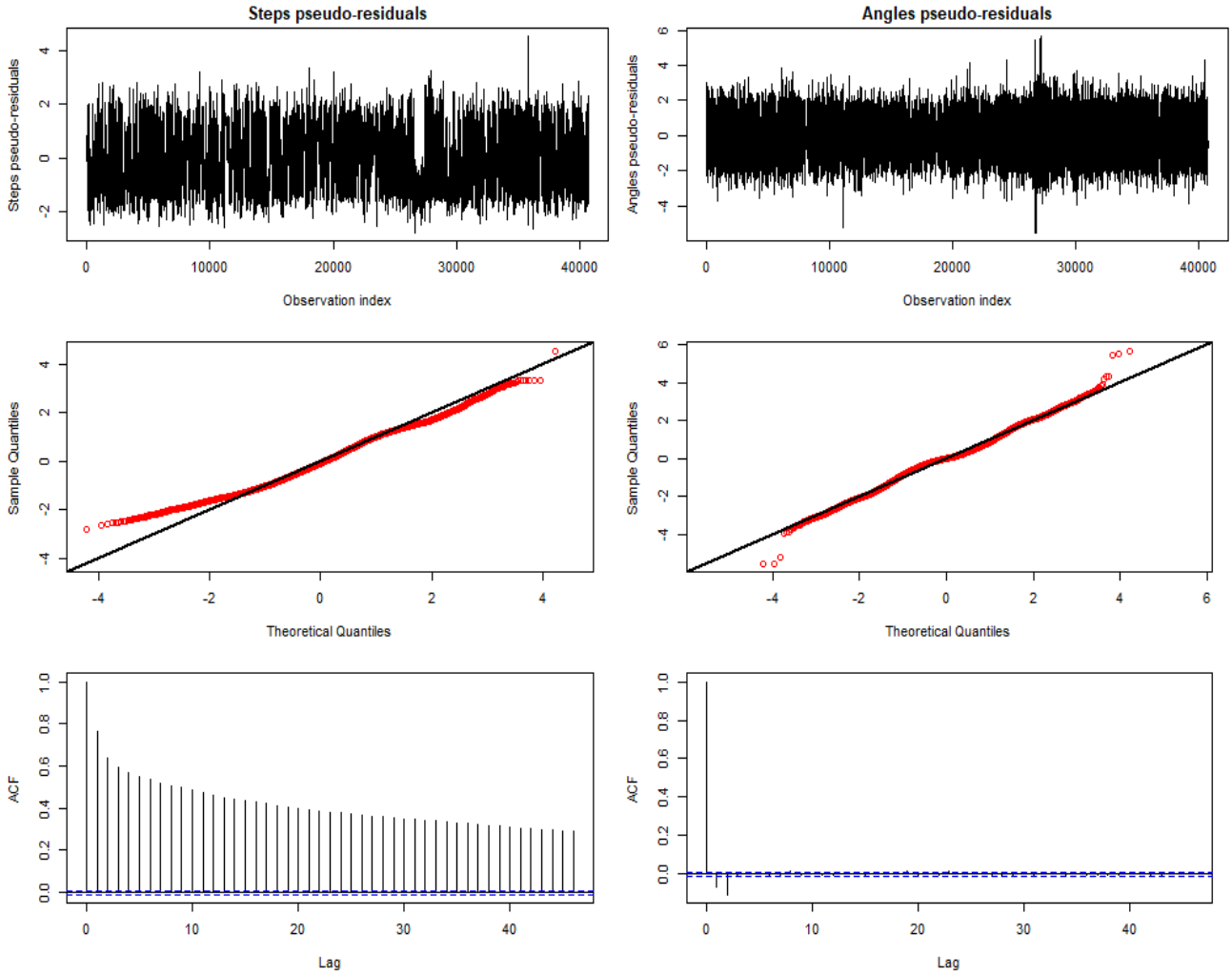


Figure S5.3. Residuals for each observation, quantiles and lags for step length and turning angle for the Hidden Markov Model using to differentiate “resting”, “foraging” and “travelling” in northern gannets *Morus bassanus.*

Table S5.2. Parameter estimates ± 95% confidence intervals (CIs) for Multi-state Markov models of likelihood of northern gannets *Morus bassanus* switching from travelling to foraging behaviour at different distances to the nearest vessel, trawler, demersal trawler, or vessel at fishing speed. **Bold** indicates a significant effect as the lower CI is > 1.

Dist. to vessel (km)	All vessels			All trawlers			Demersal trawlers			Vessels at fishing speed		
	Lower CI	Est.	Upper CI	Lower CI	Est.	Upper CI	Lower CI	Est.	Upper CI	Lower CI	Est.	Upper CI
1	0.518	1.158	2.586	0.186	1.331	9.535	0.002	0.756	351.0	0.347	0.914	2.407
2	0.792	1.190	1.788	0.197	0.777	3.067	0.142	0.969	6.603	0.574	0.975	1.655
3	0.793	1.066	1.434	0.498	1.073	2.313	0.186	0.736	2.914	0.700	1.003	1.438
4	0.889	1.115	1.399	**1.020**	**1.634**	**2.617**	0.507	1.132	2.525	0.794	1.045	1.377
5	0.838	1.028	1.262	0.802	1.239	1.913	0.440	0.891	1.790	0.722	0.926	1.188
6	0.851	1.024	1.232	0.834	1.217	1.776	0.408	0.788	1.524	0.777	0.964	1.198
7	0.886	1.050	1.245	0.829	1.155	1.608	0.568	0.963	1.631	0.825	1.004	1.221
8	0.950	1.114	1.307	0.961	1.265	1.667	0.559	0.918	1.508	0.875	1.048	1.256
9	0.956	1.115	1.301	0.905	1.162	1.492	0.614	0.949	1.465	0.844	1.004	1.194
10	0.980	1.139	1.324	0.910	1.147	1.447	0.616	0.925	1.390	0.891	1.050	1.238
11	0.940	1.091	1.268	0.895	1.113	1.385	0.619	0.903	1.318	0.871	1.023	1.202
12	0.887	1.030	1.195	0.834	1.031	1.274	0.662	0.939	1.332	0.816	0.957	1.121
13	0.876	1.018	1.181	0.859	1.049	1.282	0.697	0.963	1.330	0.828	0.967	1.129
14	0.890	1.034	1.202	0.902	1.092	1.322	0.669	0.920	1.266	0.823	0.960	1.119
15	0.881	1.025	1.193	0.916	1.100	1.322	0.675	0.918	1.250	0.828	0.963	1.121
16	0.871	1.017	1.186	0.898	1.074	1.283	0.674	0.906	1.218	0.836	0.971	1.129
17	0.862	1.008	1.179	0.900	1.071	1.273	0.663	0.886	1.184	0.828	0.962	1.117
18	0.843	0.989	1.160	0.903	1.069	1.265	0.650	0.863	1.145	0.827	0.960	1.114
19	0.830	0.977	1.149	0.936	1.103	1.300	0.636	0.839	1.108	0.784	0.910	1.056
20	0.824	0.974	1.152	0.924	1.086	1.276	0.688	0.893	1.159	0.811	0.942	1.094
21	0.845	1.005	1.196	0.923	1.082	1.268	0.668	0.862	1.113	0.795	0.923	1.073
22	0.867	1.038	1.242	0.940	1.099	1.285	0.677	0.868	1.114	0.787	0.915	1.064
23	0.843	1.014	1.219	0.933	1.089	1.272	0.691	0.879	1.119	0.795	0.926	1.078
24	0.802	0.966	1.164	0.895	1.044	1.218	0.653	0.830	1.055	0.799	0.931	1.085
25	0.782	0.946	1.143	0.867	1.011	1.178	0.652	0.826	1.045	0.801	0.935	1.092

Table S5.3. Northern gannet *Morus bassanus* diet from regurgitates sampled during annual ringing at two Icelandic colonies (Vigfúsdóttir, unpublished data). Samples were identified to species level for mackerel *Scomber scombrus* and herring *Clupea harengus,* or assigned to a higher taxonomic level or to Capelin *Mallotus villosus* or similar.

Colony	Year	Age	Number of birds	Prey category	Number of samples	Prey percentage
Hellisey	2016	Adult	1	Mackerel	1	100 %
		Chick	38	Herring	5	12.8 %
				Mackerel	33	84.6 %
				Capelin or similar	1	2.6 %
	2017	Chick	9	Mackerel	8	88.9 %
				Capelin or similar	1	11.1 %
Skrúður	2016	Adult	1	Mackerel	1	100 %
		Chick	48	Herring	30	62.5 %
				Mackerel	15	31.3 %
				Capelin or similar	2	4.2 %
				Gadoid	1	2.1 %
	2017	Adult	1	Mackerel	1	100 %
		Chick	64	Herring	44	68.8 %
				Mackerel	15	23.4 %
				Salmonid	2	3.1 %
				Unidentified fish	2	3.1 %
				Gadoid	1	1.6 %
	Total		162	Herring	79	48.5 %
				Mackerel	74	45.4 %
				Capelin or similar	4	2.5 %
				Salmonid	2	1.2 %
				Unidentified fish	2	1.2 %
				Gadoid	2	1.2 %

Chapter 6 – Reduced foraging effort at the expanding range margin could facilitate poleward shift in a colonial species

6.1 Abstract

Species distributions are shifting towards the poles in response to climate change, but not all with the same pace or pattern. In particular, colonial predators may struggle to keep pace with prey because colony formation is rare. Despite its importance, little is known about the complex process of range shifting in colonial animals. Existing colonies provide defence, mates and information, but also cause competition for food, which is reflected in foraging effort as individuals must travel further and search for longer. As such, smaller colonies can expand more quickly than larger colonies. The presence of nearby colonies also increases foraging effort due to competition, suggesting a possible benefit to being at range margins. Here we examine foraging trip duration and maximum distance from the colony in a colonial seabird (the northern gannet *Morus bassanus)*. Using data obtained from bird-borne loggers, we quantified effort across a large latitudinal gradient (48.15ºN to 71.23ºN). We collated data representing 579 breeding gannets from 20 of the 54 currently occupied colonies. Trip duration and range both increased substantially with colony size. After controlling for colony size, trip duration and range also decreased significantly with latitude suggesting suitable conditions for gannets at the northern edge of their range but poor conditions at the southern edge. Lower foraging effort at the expanding range margin may allow distribution shift in colonial species in response to environmental change if the barriers to colony formation can be overcome.

Keywords: Climate change; range shift; latitudinal gradient; central place foraging; coloniality; species distributions; bio-logging; seabird; fish; marine

6.2 Introduction

Average global temperatures are rising (Parmesan & Yohe, 2003), with many species responding by moving to higher latitudes (Chen *et al.,* 2012; Hickling *et al.,* 2006; Thomas & Lennon, 1999). However, not all species shift at the same pace or with the same pattern. Contrasting range shift patterns may cause spatial or temporal mismatches between consumers and their food sources (Renner & Zohner, 2018; Schweiger *et al.,* 2008). In particular, site-faithful colonial predators may struggle to follow their prey (Matthiopoulos *et al.,* 2005; Reed & Levine, 2005). Colonial breeding is common among vertebrates (Danchin & Wagner, 1997), yet we have a poor understanding of the factors affecting how the distributions of colonial animals respond to global climate change (Grémillet & Boulinier, 2009).

Colonial seabirds have limited breeding sites that provide both access to suitable marine foraging areas and safety from terrestrial predators (Rolland *et al.,* 1998). Climate change is considered one of the top three threats to seabirds (Dias *et al.,* 2019). The main climate-related threat to seabirds is thought to be reduced prey availability (Sydeman *et al.,* 2012), especially during the breeding season (Bertram *et al.,* 2009; Le Bohec *et al.,* 2008; Thackeray *et al.,* 2010). Many seabird prey species are shifting poleward (Arnott & Ruxton, 2002; Atkinson *et al.,* 2019; Perry *et al.,* 2005), along with some seabird populations (Barrett *et al.,* 2017; Crawford *et al.,* 2015; Dunlop, 2009; Munilla *et al.,* 2016). However, seabirds may struggle to keep pace because individuals are generally faithful to their breeding sites even when local conditions are no longer optimal (Bried & Jouventin, 2002). As such, range shifting requires individuals to disperse away from their natal or breeding colony to form a new colony. Such events are rare (Kildaw *et al.,* 2005; Munilla *et al.,* 2016) because both natal and breeding dispersal in seabirds is infrequent (Coulson, 2002). Established colonies provide suitable mates (Wells *et al.,* 1998), defence against predators (Oro *et al.,* 2006), public information about breeding success (Forbes & Kaiser, 1994), and social information about food (Evans *et al.,* 2016; Ward & Zahavi, 1973). Colony formation is, therefore, only likely when the benefits of joining established colonies outweigh the costs of poor local conditions and density-dependent factors (Crespin *et al.,* 2006; Dunlop, 2009). These include competition for food (Birt *et al.,* 1987) and nest sites (Kildaw *et al.,* 2005), along with parasite and pathogen burden (Boulinier & Danchin, 1996). Despite these costs, isolated nests

are scarce, and so sites must often support a threshold number of roosting individuals before birds attempt to breed (Coulson, 2002), and even more for attempts to be successful (Juáres *et al.,* 2017).

Very small colonies are initially vulnerable to Allee effects, where individual fitness is lower for those in smaller populations (Courchamp *et al.,* 1999; Péron *et al.,* 2010), but, once established, small colonies can grow quickly due to low levels of competition (Dunlop, 2009; Kildaw *et al.,* 2005). With rapid growth, prey becomes depleted around colonies (Birt *et al.,* 1987), thereby increasing average foraging effort (Piatt *et al.,* 2007). As such, colonies of intermediate size generally have higher fecundity than very small or large colonies (Brown *et al.,* 1990; Oro *et al.,* 2006) and are attractive to prospectors (Dunlop, 2009). Foraging effort provides a good metric for resource competition, illustrated by the fact that foraging trips tend to be much longer at large colonies (Ashmole, 1963; Jovani *et al.,* 2016; Lewis *et al.,* 2001; Oppel *et al.,* 2015), and during years of low food availability (Hamer *et al.,* 2007; Davies *et al.* 2013; Paiva *et al.,* 2013; Thorne *et al.,* 2015; Warwick-Evans *et al.,* 2016a). In the extreme, limited prey availability can override the effect of colony size (Lewis *et al.,* 2006). When the foraging effort of individuals approaches their energetic limits, this can constrain colony size (Ballance *et al.,* 2009), as indicated by large colonies having low reproductive success (Hunt Jr. *et al.,* 1986; Tims *et al.,* 2004) and lower per capita growth rates (Davies *et al.,* 2013; Barbraud *et al.,* 2018). Furthermore, competition with birds from nearby colonies can increase foraging effort (Wakefield *et al.,* 2013; Corman *et al.,* 2016) and limit colony size (Ainley *et al.,* 2003; Cairns, 1989; Furness & Birkhead, 1984). Consequently, range-shifting in colonial seabirds should proceed in a stepwise manner, consisting of rapid jumps when new colonies form, followed by periods of stasis (Holt, 2003; Matthiopoulos *et al.,* 2005). This is important as prey are not tied to colonies and may, therefore, shift with a different pattern. Despite this hypothesis, little is known about how seabird distributions respond to climate change (Grémillet & Boulinier, 2009; Sydeman *et al.,* 2012) or how foraging effort varies across large spatial gradients.

The northern gannet *Morus bassanus* (hereafter “gannet”), a North Atlantic breeding seabird, provides a well-documented example of range expansion in a colonial predator. During the last century, the global population increased significantly on both sides of the Atlantic after release from long-term human persecution (Serjeantson, 2001), and they are recolonising parts of their

prehistoric range (Montevecchi & Hufthammer, 1990). New colonies have formed recently (Montevecchi & Myers, 1997; Murray *et al.,* 2015a), and grown faster than more established ones (Moss *et al.,* 2002). The population has increased across its range within the last century. Since 1935, the distribution of gannetries has expanded south by 0.4º latitude (2.7º considering only the East Atlantic) and north by 7.7º (Wynne Edwards *et al.,* 1936; Grémillet *et al.,* 2006; Barrett *et al.,* 2017). The first Norwegian gannet colony in recorded history formed in 1946 at 62.4ºN and several others have since become established further north, with the newest colony, which was established in 2011 at 74.2ºN, being the world's northernmost (Barrett *et al.,* 2017). Some of the new colonies have since been abandoned (zero nests counted), but the overall Norwegian population is growing (Barrett *et al.,* 2017), and short foraging trips suggest good conditions (Pettex *et al.,* 2012; 2015). This spread coincided with an inflow of unusually warm waters and, with them, gannet prey species including herring *Clupea harengus* and mackerel *Scomber scombrus* (Berge *et al.,* 2015; Dalpadado *et al.,* 2012). Similarly, a recent influx of mackerel in Iceland associated with warmer waters has provided a new food source (Astthorsson *et al.,* 2015; Vigfúsdóttir *et al.,* 2009). Conversely, near to the southern edge of the distribution of the gannet, years of warmer sea temperature have been associated with lower breeding success and longer foraging trips (Montevecchi *et al.,* 2013; Warwick-Evans *et al.,* 2016a). Therefore, climate change appears to be improving conditions for gannets in the north but not in the south of their range. If foraging effort were related only to intraspecific competition, we would expect lower foraging effort for a given colony size at all edges of the species range. However, if optimal conditions are shifting, we would expect foraging effort to be lowest at the edge with an improving climate, when controlling for colony size.

Here, we explored how latitude and colony size influence foraging effort derived from satellite tracking for 20 of the 54 known gannetries, which support 70% of the global population (Murray *et al.,* 2015a). These colonies span 84% of the gannet's latitudinal extent, providing the first opportunity to investigate seabird foraging effort across such a large spatial gradient (48.15ºN to 71.23ºN). First, we predict colony size will be the main driver of effort with longer trips at larger colonies (Davies *et al.,* 2013; Lewis *et al.,* 2001). Second, if suitable climatic conditions are shifting northwards, when controlling for the effect of colony size, we predict that foraging trips will be shorter at high latitude colonies.

6.3 Methods

6.3.1 Foraging trip duration and range

We collated mean foraging trip duration and foraging range (maximum distance from the colony) for 20 colonies, derived from >5,000 tracked trips for 579 chick-rearing gannets. To our knowledge, there are no other gannetries for which satellite tracking data are available. Ranging from 48.15ºN to 71.23ºN, they span 84% of the latitudinal extent of breeding colonies from Cape St. Mary's, Newfoundland, at 46.83ºN to Bjørnøya, Svalbard, at 74.21ºN (Barrett *et al.,* 2017; Chardine *et al.,* 2013; Figure 6.1). Sea surface temperatures are generally lower at higher latitudes, and while there are large differences in the winter temperatures between East and West Atlantic colonies, summer temperatures are more similar (Figure S6.1). We used published means for seven colonies and calculated means from tracking data for 13 (Figure 6.1, Table 6.1, Table S6.1). When we had data from multiple years, we used the mean across all trips unless otherwise indicated. Global Positioning System (GPS) data were available for all sites except St Kilda, where data were from Platform Transmitter Terminal (PTT) devices (locations via the ARGOS satellite systems with a median of 75 minutes between locations; Wakefield *et al.,* 2013). PTTs are less likely to record at regular intervals compared to GPS loggers (Wilson *et al.,* 2002), so we removed foraging trips with poor data quality (one trip with only two records and 12 with location intervals over three hours). Total distance travelled was recorded but not analysed as the frequency of recorded locations, which varied from 1 second to ~180 minutes (Table S6.1), impacts total distance more than duration or range.

6.3.2 Colony size

We collated published counts of apparently occupied sites or nests for 2004–17 for the nearest available year to that of the tracking data, with a mean difference of 2 years (Table 6.1; Table S6.1). Recent counts estimate a global northern gannet population of 525,694 apparently occupied nests across 54 colonies (Murray *et al*., 2015a). Our study includes data from 20 colonies with a combined estimated population of 368,308 nests, covering 37% of currently occupied colonies and an estimated 70% of individuals worldwide (Table 6.1). Tracking in the Vestmannaeyjar archipelago took place only on Hellisey, but as Hellisey is within 5km of the other gannetries, we combined their population counts

(Garðarsson, 2019). Similarly, we included Les Etacs and Ortac in Alderney as a single colony due to their 6km proximity.

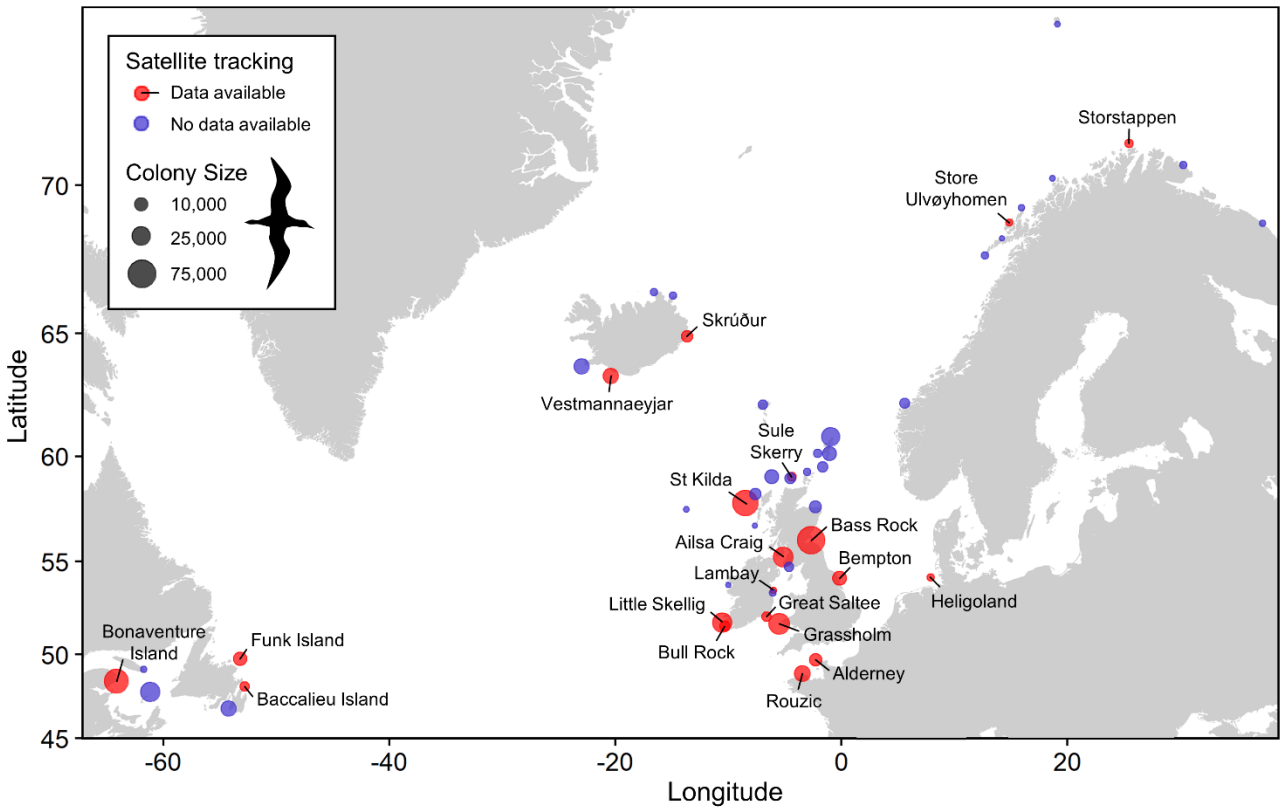


Figure 6.1. Northern gannet *Morus bassanus* colonies with circles proportional to colony size. For labelled colonies (red), foraging data from satellite tracking is included in this study, whereas for unlabelled colonies (blue) it is not. Map adapted from tiles by Stamen Design, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

Table 6.1. Mean foraging trip metrics and colony counts for 20 northern gannet *Morus bassanus* colonies ordered by latitude. Values are given ± SD where available. See Table S6.1 for longitude, years of counts and tracking data, sampling frequency, sample size, and total distance travelled.

Colony	Lat.	Mean duration (h)	Mean range (km)	n birds	Source of tracking data	Count (AOS/ AON)	Source of colony count
Baccalieu Is.	48.15	9.3 ± 7.3	39.9 ± 24.7	6	Montevecchi *et al.,* 2012b*	2253	Chardine *et al.,* 2013
Bonaventure	48.48	28	132	14	Garthe *et al.,* 2006	53635	
Rouzic	48.90	17.7 ± 8.5	100 ± 35	20	Grémillet *et al.,* 2006	17507	Grémillet *et al.,* 2006
Alderney	49.71	23.0	122.0	60	Warwick-Evans *et al.,* 2016a	7885	Murray *et al.,* 2015a
Funk Is.	49.75	16.5	102.6	26	Garthe *et al.,* 2011	10047	Chardine *et al.,* 2013
Bull Rock	51.58	11.9 ± 8.1	69.8 ± 34.1	14	Wakefield *et al.,* 2013*	3694	Wanless *et al.,* 2005a
Grassholm	51.73	21.2 ± 15.2	108.9 ± 57.9	172	Clark *et al.,* unpubl. data	36011	Murray *et al.,* 2015b
Little Skellig	51.78	13.4 ± 11.8	96.5 ± 61.8	9	Wakefield *et al.,* 2013*	29683	Wanless *et al.,* 2005a
Great Saltee	52.11	15.5	83.7	23	Wakefield *et al.,* 2013* & Hamer *et al.,* 2001	2446	
Lambay	53.50	11.6 ± 7.6	37.5 ± 19.6	3	Wakefield *et al.,* 2013*	138	JNCC, 2010
Bempton	54.15	8.6	43.0	25	Langston *et al.,* 2013	11061	JNCC, 2012
Heligoland	54.18	7.9 ± 8.0	42.0 ± 45.7	3	Garthe *et al.,* 2017	656	Murray *et al.,* 2015a
Ailsa Craig	55.25	26.2 ± 16.2	152.3 ± 70.5	16	Wakefield *et al.,* 2013*	33226	
Bass Rock	56.08	27.8 ± 15.8	158.4 ± 69.1	28		60953	JNCC, 2009
St. Kilda	57.86	24.3 ± 14.8	164.2 ± 124.1	21		60290	Murray *et al.,* 2015a
Sule Skerry	59.08	14.4 ± 5.9	72.9 ± 19.8	2		1870	
Vestmann-aeyjar	63.36	10.2 ± 7.4	43.0 ± 27.0	9	Clark *et al.,* 2019	15044	Garðarsson, 2019
Skrúður	64.90	4.8 ± 4.5	29.2 ± 24.2	27		6051	
Store Ulvøyhomen	68.85	6.9	22.3	43	Pettex *et al.,* 2012	308	Barrett *et al.,* 2017
Storstappen	71.23	6.6	38.7	58		1244	

AOS = Apparently occupied sites, AON = Apparently occupied nests; JNCC = Joint Nature Conservation Committee Seabird Monitoring Program database (http://jncc.defra.gov.uk/smp/ Accessed 14/1/19); *Mean values were not available in the published sources, so tracking datasets were provided by the authors.

6.3.3 Statistical analysis

We tested the effects of colony size and latitude on mean foraging trip duration and range using Linear Models. We square-root transformed colony counts as relationships between mean trip duration and the square-root of colony size are approximately linear (Lewis *et al.,* 2001) because foraging area (km^2) increases in relation to the square of range (km) (Gaston *et al.,* 2007). Shapiro-Wilk normality tests did not show deviation from a normal distribution for mean duration ($W = 0.92$, $p = 0.14$) or range ($W = 0.92$, $p = 0.08$). We sampled 37% of the 54 known colonies (Murray *et al.,* 2015a), and the standard error of the mean is overestimated if sampling a large proportion (over 10%) of the total population, so we applied the finite population correction (Cochran, 1977). We chose a conservative upper estimate of 60 colonies worldwide and implemented the correction in the 'survey' R package's 'svyglm' function (Lumley, 2004). We used the Rao-Scott working likelihood test for model selection, using the default linear combination of F distributions with 17 denominator degrees of freedom to generate the likelihood ratio (Lumley and Scott, 2014). We calculated adjusted pseudo r^2 values in the 'jtools' R package (Long, 2019), and delta (Δ) pseudo r^2 values for each explanatory variable to compare their relative importance. We also ran these models excluding the six colonies for which fewer than ten individuals were tracked (Table S6.2). We did not test for an interaction due to the small sample size.

For eight colonies, mean values from multiple years of tracking data were available. For these annual means, we fitted Linear Mixed Models explaining trip duration and range in relation to colony size and latitude, with colony ID fitted as a random intercept using the 'lme4' R package (Bates *et al.,* 2014). We only included data sampled using a minimum GPS frequency of three minutes (this excluded St Kilda and Heligoland, see Table S6.3). The finite population correction could not be applied to the standard error, confidence intervals or p values as mixed effects models were not available in 'svyglm' (Lumley, 2004) or any other published package.

Foraging range for all colonies was previously inferred from trip duration using satellite telemetry data from one colony as birds from only one colony had been tracked at that time (Davies *et al.,* 2013; Hamer *et al.,* 2000; Lewis *et al.,* 2001). We also tested how well trip duration predicts foraging range using a standard Linear Model, and a Linear Model with a fixed zero intercept to provide

a comparison with the inferred ranges reported in Lewis *et al.* (2001) with results given in Figure S6.2.

6.4 Results

6.4.1 Mean trip duration and range for each colony

Foraging trip durations and ranges across 20 colonies increased substantially with colony size and decreased with latitude, with square-root colony size explaining more of the variation than latitude as shown by the Δ pseudo r^2 values (Table 6.2; Figure 6.2). Linear Models including both square-root colony size and latitude had a pseudo adjusted r^2 of 0.71 for foraging trip duration and 0.76 for foraging range. Results were similar when excluding the six colonies for which fewer than ten birds were tracked, but with higher Δ pseudo r^2 value for the latitude effect of 0.10 for duration and 0.06 for range (Table S6.2).

Table 6.2. Parameter estimates for Linear Models fitted with the finite population correction explaining northern gannet *Morus bassanus* colony means for foraging trip duration and range (maximum distance from the colony) for 20 colonies. Delta (Δ) pseudo adjusted r^2 is the difference in pseudo adjusted r^2 between the models with and without the explanatory variable included and is thus a measure of the contribution of each variable to explaining the variation in foraging effort.

Foraging effort	Explanatory variable	Estimate ± standard error	95% confidence intervals	2log LR	d. f.	p value	pseudo r^2 Δ
Trip duration (h) ~	Intercept	23.29 ± 6.02	11.48, 35.09	-	-	-	-
	√Colony size	0.070 ± 0.008	0.054, 0.085	77.53	1,17	<0.001	0.49
	Latitude	-0.276 ± 0.097	-0.466, -0.087	8.16	1,17	0.012	0.06
Foraging range (km) ~	Intercept	102.76 ± 34.94	34.28, 11.24	-	-	-	-
	√Colony size	0.467 ± 0.048	0.374, 0.560	96.51	1,17	<0.001	0.58
	Latitude	-1.244 ± 0.554	-2.330, -0.158	5.04	1,17	0.040	0.03

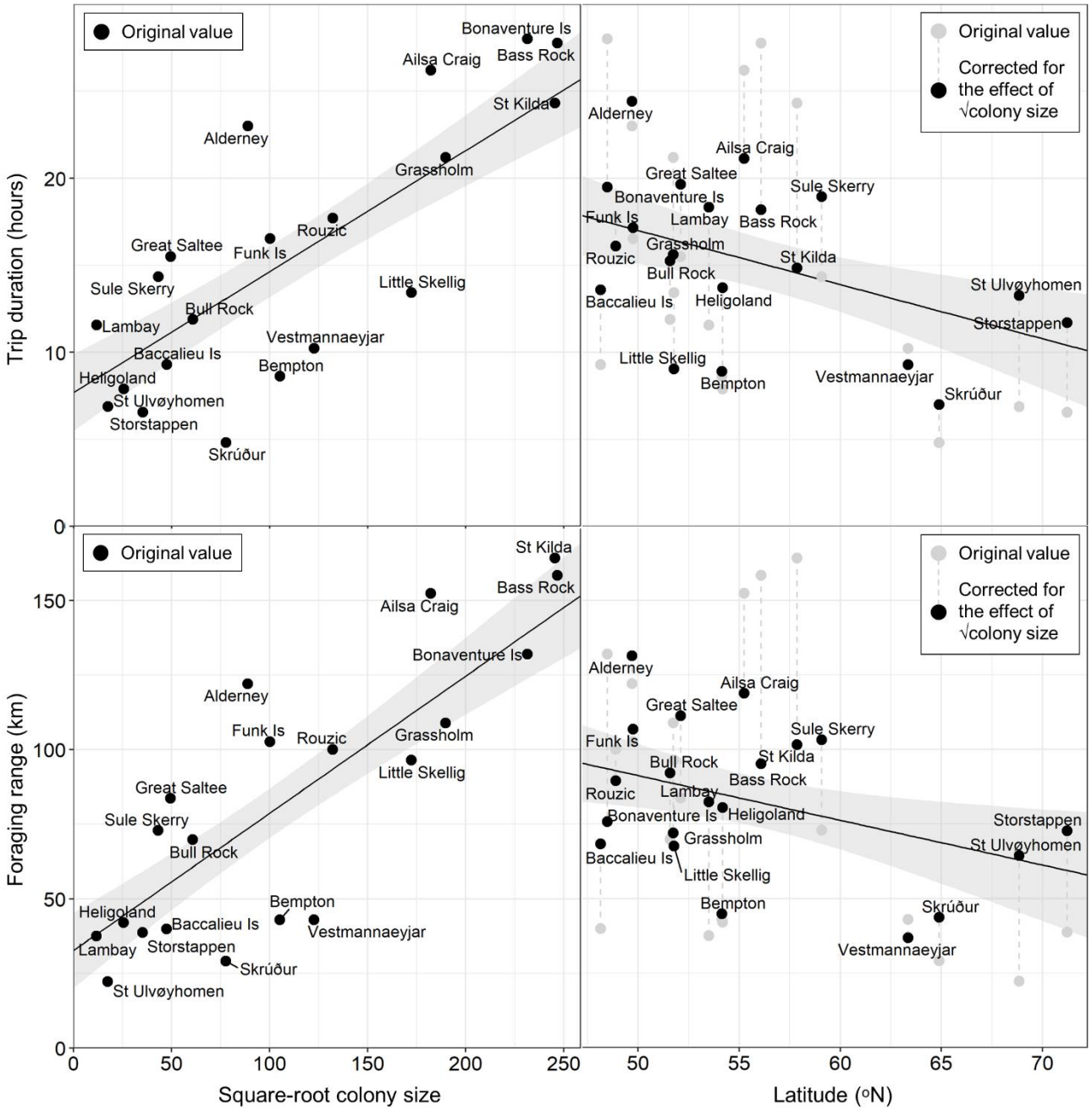


Figure 6.2. Mean foraging trip duration and range (maximum distance from the colony) for 20 northern gannet *Morus bassanus* colonies in relation to colony size and latitude, labelled with colony name. Black lines show the prediction from a finite population corrected Linear Model ± 95% confidence intervals (grey ribbon) using the mean value of latitude to predict the effect of square-root (√) colony size and vice versa. To correct for √colony size, we subtracted the √colony size effect from each datapoint (grey circle) and then added the √colony size effect for the mean √colony size (black circle). Consequently, the estimates for larger colonies decrease and smaller colonies increase.

6.4.2 Mean trip duration and range for each year

For 37 annual means across 18 colonies, Linear Mixed Models including the foraging trip metrics split by year showed similar strong positive relationships with colony size and smaller negative relationships with latitude (Table 6.3, Figure 6.3). For foraging trip duration, the inter-colony variance ± standard deviation of 19.560 ± 4.423 (67%) was greater than the interannual variance of 9.777 ± 3.127 (33%). However, for foraging range, the inter-colony variance of 373.0 ± 19.31 (47%) was less than the interannual variance of 423.3 ± 20.57 (53%).

Table 6.3. Parameter estimates from Linear Mixed Models for northern gannet *Morus bassanus* annual colony means for foraging trip duration and range (maximum distance from the colony), with colony fitted as a random intercept. Reported p values are overestimated as they are not corrected for the finite population.

Foraging effort	Explanatory variable	Estimate ± standard error	95% confidence intervals	F statistic	p value
Trip duration (h) ~	Intercept	28.97 ± 10.38	8.63, 49.32	-	-
	√Colony size	0.064 ± 0.018	0.029, 0.099	12.538	0.002
	Latitude	-0.371 ± 0.166	-0.696, -0.046	4.979	0.041
Foraging range (km) ~	Intercept	137.21 ± 56.57	26.33, 248.09	-	-
	√Colony size	0.410 ± 0.097	0.220, 0.600	17.957	<0.001
	Latitude	-1.822 ± 0.920	-3.625, -0.019	3.920	0.066

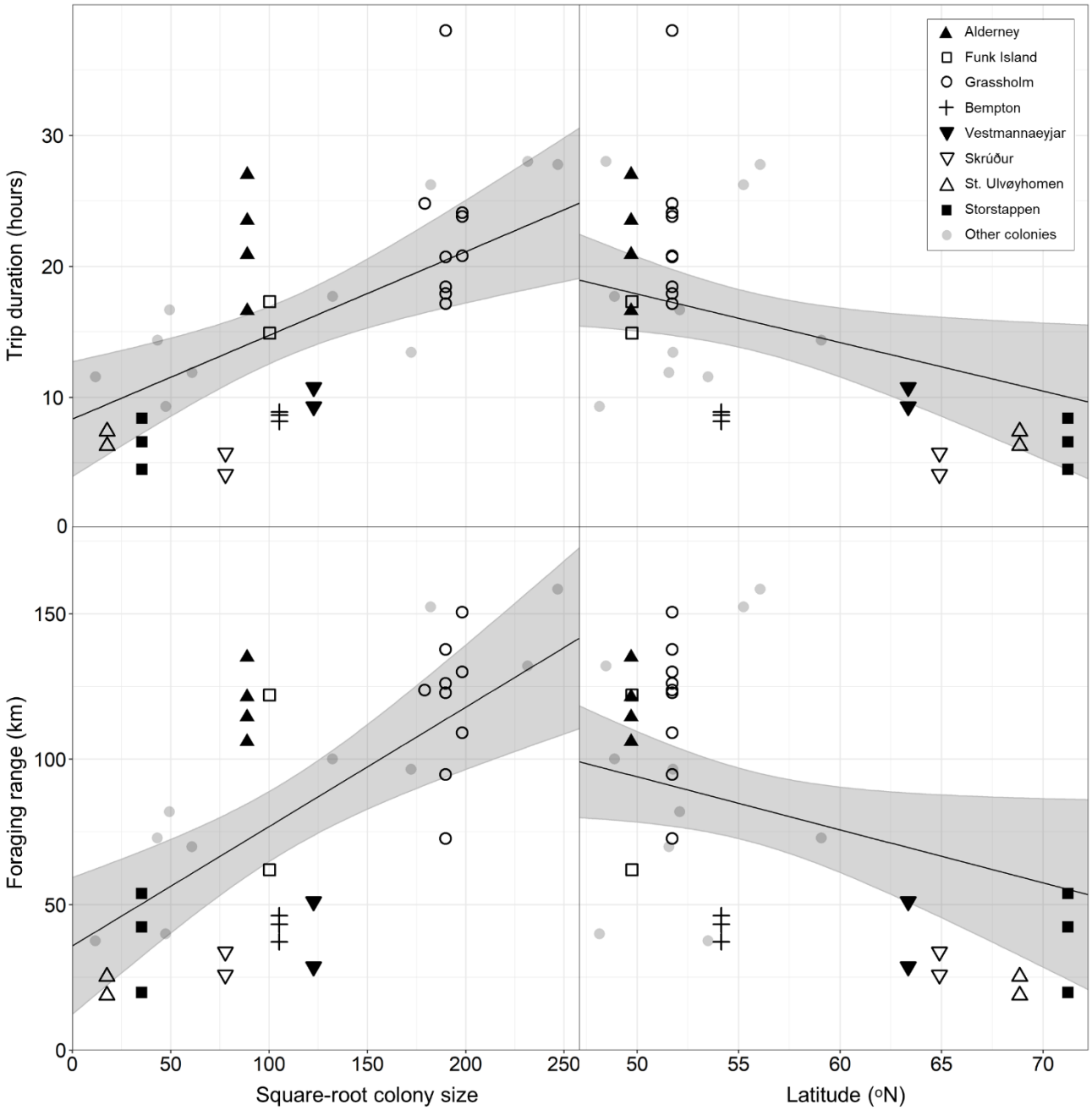


Figure 6.3. Annual mean foraging trip duration and range (maximum distance from the colony) for 18 northern gannet *Morus bassanus* colonies in relation to colony size and latitude, with black shapes indicating colony. Grey circles indicate that only one year of data is available. Black lines show the prediction from a Linear Mixed Model with colony fitted as a random intercept ± 95% confidence intervals (grey ribbon) using the mean value of latitude to predict the effect of square-root colony size and vice versa.

6.5 Discussion

We investigated how colony size and latitude influenced foraging trip duration and range in breeding gannets (measured by bird-borne loggers) during a period of poleward range expansion. As expected, there was a strong positive relationship between foraging effort and colony size. After controlling for this, we found that foraging effort decreased with latitude and, consequently, proximity to the expanding edge of the spatial distribution of the species. We discuss how these results provide a rare insight into the way that colonial species may respond to environmental change.

6.5.1 Foraging effort, colony size and latitude

The combined effects of colony size and latitude explained most of the variation in mean foraging trip duration (pseudo adjusted r^2 = 0.67) and foraging range (pseudo adjusted r^2 = 0.71). Colony size was the main driver of foraging trip duration (Δ pseudo adjusted r^2 = 0.49) and range (Δ pseudo adjusted r^2 = 0.57; Figure 6.2; Davies *et al.,* 2013; Lewis *et al.,* 2001), likely due to intra-specific competition for food (Ashmole, 1963; Birt *et al.,* 1987; Jovani *et al.,* 2016; Oppel *et al.,* 2015). This relationship was clear even though many of the sampled colonies are still growing (Murray et al., 2015a). We found that interannual variance accounts for 33% of the variance in trip duration and 53% in range, showing that changing local conditions have a substantial impact on foraging effort (Table 6.3, Figure 6.3). The slope for square-root colony size and trip duration of 0.072 was similar to the slope of 0.069 inferred from vantage point observations of gannet trip durations in 2000 (Lewis *et al.,* 2001). However, these slopes were both steeper than the slope of 0.011 (smaller effect of colony size) inferred from vantage point observations in 2009 (Davies *et al.,* 2013). The variation in slope appears to be due to greater variation in foraging effort at larger colonies (Hamer *et al.,* 2006), suggesting that individuals in large colonies are more affected by changing environmental conditions (Davies *et al.,* 2013). Greater interannual variation for larger and lower latitude colonies (Figure 6.3; Davies *et al.,* 2013) indicates that individuals are closer to their energetic limits (Gaston *et al.,* 2007), but this needs further investigation.

Colony size is not the only factor influencing foraging effort – we detected a latitudinal gradient in foraging trip durations (Δ pseudo r^2 = 0.06) and ranges (Δ pseudo r^2 = 0.03). The reason that individuals from colonies at the edge of the

range have lower foraging effort after controlling for colony size are unclear but may be related to reduced inter-colony competition because foraging trip length increases with the number and size of nearby colonies (Ainley *et al.,* 2003; Cairns, 1989; Furness & Birkhead, 1984; Wakefield *et al.,* 2013). While this would suggest that all edges are equally beneficial, we found shorter trip durations and smaller foraging ranges nearer to the northern edge but not the southern edge of the gannet's distribution (Figure 6.2; Grémillet *et al.,* 2006; Pettex *et al.,* 2015), indicating that optimal environmental conditions are shifting northwards. Specifically, Lambay and Heligoland in the south were colonised at a similar time to Storstappen and Store Ulvøyhomen in the north, and are similar sizes, but birds from the southerly colonies do not show lower foraging effort than expected for their size, while those from the northerly colonies do (Figure 6.1, Table 6.1). Furthermore, birds from both Icelandic colonies show low foraging effort even though Vestmannaeyjar has been occupied since the 1750s, while Skrúður was only colonised in 1947 (Gurney, 1913). The effect of local environmental conditions can outweigh that of competition, as shown in Cape gannets *Morus capensis*, which are experiencing dramatic population decline and as a consequence, the relationship between colony size and foraging trip duration has been inverted (Lewis *et al.,* 2006).

At high latitudes, warming seas have been associated with influxes of warm-water pelagic fishes, potentially aiding gannet colonisation (Astthorsson *et al.,* 2015; Barrett, 2007; Barrett *et al.,* 2017; Berge *et al.,* 2015). By contrast, at low latitudes, warm waters are linked to high foraging effort and low breeding success on both sides of the Atlantic (Montevecchi *et al.,* 2013; Warwick-Evans *et al.,* 2016b). Furthermore, heat or cold stress at the nest (Hochscheid *et al.,* 2002), can influence breeding success (Reid *et al.,* 2000) and species distributions (Oswald *et al.,* 2011). As such, warming climates may present a threat to gannets at low latitudes while providing an opportunity at high latitudes. Northerly colonies with low foraging effort could grow more rapidly through increased breeding success and attracting prospectors (Moss *et al.,* 2002). However, there has not been a recent poleward shift in gannet breeding colonies in the West Atlantic. This is likely due to the placement of the Gulf Stream (Sato *et al.,* 2014), leading to greater differences in temperature in the West compared to the East Atlantic as latitude increases (Figure S6.1). In summary, competition within colonies explains why effort increases with colony size, while competition

between colonies explains why effort may be lower at range edges. However, edges are not all equally favourable, and shifting climatic conditions explain why effort is lowest at the poleward range edge.

Understanding gannet foraging ecology at high latitudes is timely because most North Atlantic seabirds have suffered declines in recent years, possibly linked to reduced food availability or quality driven by climate warming (Carroll *et al.,* 2015; Frederiksen *et al.,* 2013; Sandvik *et al.,* 2005; Wanless *et al.,* 2005b). Most North Atlantic seabirds rely on forage fish, including sandeels *Ammodytes marinus* and capelin *Mallotus villosus* (Lilliendahl & Solmundsson, 1997), but warming reduces sandeel availability (Arnott & Ruxton, 2002). Furthermore, Iceland and Norway have seen recent influxes of mackerel *Scomber scombrus* (Astthorsson *et al.,* 2015; Berge *et al.,* 2015), which both competes with and predates on sandeels and capelin (Óskarsson *et al.,* 2016). Similarly, increased herring *Clupea harengus* abundance has been linked to capelin stock collapse and consequent black-legged kittiwake *Rissa tridactyla* decline in Norway (Barrett, 2007). These losses heavily impact small seabirds, but gannets are large with a broad diet (Lewis *et al.,* 2003), and so mackerel and herring are suitable replacements (Vigfúsdóttir *et al.,* 2009). As such, flexibility in foraging effort and diet may explain why gannets thrive while other North Atlantic seabirds struggle.

6.5.2 Implications for poleward shift in colonial species

Our results show lower foraging effort at the expanding edge of a species distribution. Low foraging effort can translate into higher survival or breeding success (Paiva *et al.,* 2013), or may attract prospectors. This may provide a mechanism for rapid poleward range shift in colonial species in a stepwise pattern, potentially jumping large distances across their highly fragmented breeding habitat. For example, Cory's shearwaters *Calonectris borealis* recently expanded their range northwards by forming new colonies distant from natal colonies (Munilla *et al.,* 2016). However, in other species, new colonies form close to existing ones (Burg *et al.,* 2003; Kildaw *et al.,* 2005). Even without new colony formation, emigration from colonies with high foraging effort to those with lower effort would allow the average latitude of an individual within the population to increase. This could apply to any species where recruits are attracted to conspecifics, as this process inhibits empty patch colonisation but reduces patch extinction due to repeated immigration, an effect that becomes stronger in more

fragmented habitats (Reed & Levine, 2005). As competition at existing colonies encourages dispersal, a growing core population may be needed to facilitate colony formation and consequent poleward shift (Crespin *et al.,* 2006). However, dispersal is also more likely when environmental conditions at the natal colony are poor (Dunlop, 2009).

A better understanding of range-shifting in colonial species may help mitigate the impacts of climate change, as we may be able to predict suitable future areas for monitoring and protection (Grémillet & Boulinier, 2009). Particularly as seabirds are typically under-represented (Poloczanska *et al.,* 2013) or excluded from large-scale multi-species analyses (Root, 1988; Thomas & Lennon, 1999; VanDerWal *et al.,* 2013). Conservation methods such as translocations (Priddel *et al.,* 2006), decoys and playbacks (Podolsky & Kress, 1989) can attract recruits to potential new colonies. These interventions may enable species to shift into more climatically suitable regions, but only if prey is available. Moreover, realised distributions are limited by more than just climate and food availability. For example, southward-shifting seabirds in Australia and Africa are reaching the limits of the available coastline required for breeding, unlike their marine prey (Crawford *et al.,* 2015; Dunlop, 2009). Seabirds may also be restricted to suitable wave and wind regimes (Suryan *et al.,* 2008). Additionally, visual predators are constrained by light, which drives the wintering distributions of Greenland great cormorants *Phalacrocorax carbo* (White *et al.,* 2013) and Ross Island Adélie penguins *Pygoscelis adeliae* (Ballard *et al.,* 2010) because the timing of migrating to escape the polar night relates to breeding colony latitude. However, long summer days provide more foraging opportunities (Hill *et al.,* 2003; Watanabe *et al.,* 2012), and this is likely to benefit gannets as they rarely fly at night and their activity levels correlate with day length (Furness *et al.,* 2018).

6.6 Conclusion

Gannets breeding in high-latitude colonies had lower foraging effort than in low-latitude colonies when controlling for colony size. This may be related to differences in competition and food availability among colonies and, moreover, help explain why colonies at the expanding range margin can grow rapidly. Our results support the assertion that optimal conditions for marine predators are shifting poleward and, specifically, that warming boreal seas provide good

environmental conditions for gannets. Measuring behaviour offers a useful tool to identify proximate mechanisms of distribution change, but we still do not understand how new colonies form. In general, we know very little about how range shifting relates to colonial breeding, but accounting for coloniality is key to understanding, predicting and mitigating the impacts of climate change for these species.

6.7 Supplementary material

Figures S6.1 shows North Atlantic sea surface temperatures. Table S6.1 contains additional data for the 20 gannet colonies. Figures S6.2 shows the relationship between trip duration and foraging range. Table S6.2 gives model estimates for colonies for which >10 individuals were tracked. Table S6.3 gives the values derived from GPS data and colonies counts separated by year.

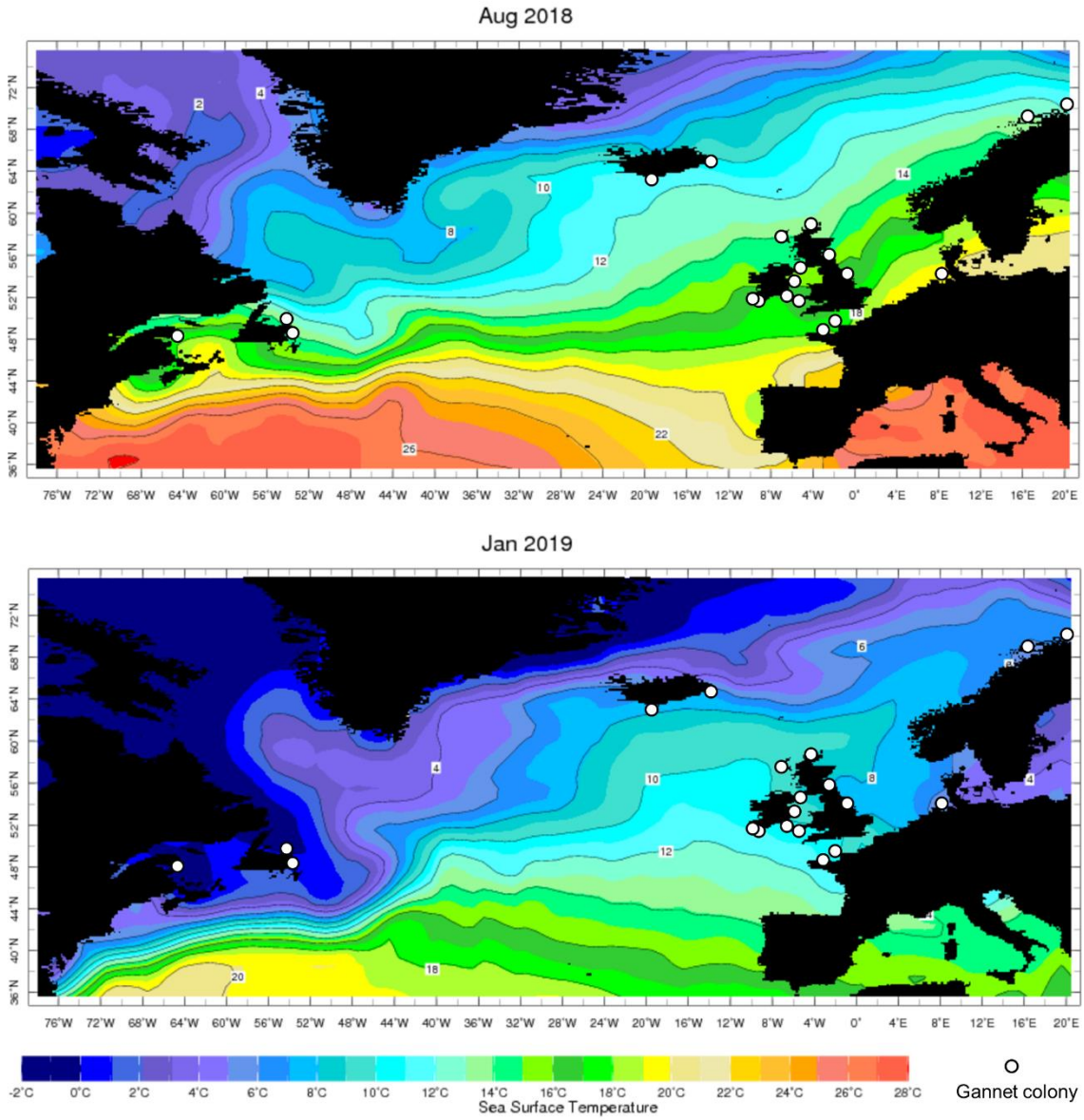


Figure S6.1. Mean sea surface temperature contours for the North Atlantic in August and January in 2018 showing the approximate locations of gannet colonies included in this study. Temperatures are from Reynolds and Smith OISST version 2 sea surface temperature dataset, maps produced by the International Research Institute for Climate and Society, Colombia University, accessed at https://iridl.ldeo.columbia.edu/maproom/Global/Ocean_Temp/Monthly_Temp.

Table S6.1. Additional information for the 20 northern gannet colonies included in this study ordered from low to high latitude. Trip metrics shown as means ± standard deviation where available.

Colony	Lon	Colony count year	GPS years	Tracking frequency	n trips	Total distance (km)
Baccalieu Is.	-52.80	2009	2009	?	18	141.61 ± 112.14
Bonaventure	-64.15	2004	2003	3 min	15	432
Rouzic	-3.44	2005	2005	10 sec	20	479 ± 206
Alderney	-2.24	2011	2011,13–15	2 min	288	407.8
Funk Island	-53.18	2004	2003/05	3 min	34	296.06
Bull Rock	-10.3	2004	2011	2 min	166	212.20 ± 131.85
Grassholm	-5.48	2015	2013–17	1 or 2 min	269	360.44 ± 238.67
Little Skellig	-10.5	2004	2011	2 min	64	246.18 ± 189.94
Great Saltee	-6.62	2004	1999/2011	2 or ~180 m	216	265.80 ± 177.58*
Lambay	-6.0	2010	2011	2 min	37	126.82 ± 75.25
Bempton	-0.17	2012	2010–12	10s or 2m	2791	127.4
Heligoland	7.92	2014	2014	Unknown	168	124.6 ± 138.6
Ailsa Craig	-5.12	2014	2011	2 min	111	485.96 ± 264.82
Bass Rock	-2.64	2009	2011	2 min	124	503.38 ± 250.43
St Kilda	-8.48	2013	2010	~75 min	254	459.78 ± 346.12
Sule Skerry	-4.40	2013	2011	2 min	14	246.68 ± 92.62
Vestmannaeyjar	-20.37	2013/14	2016/17	1 or 2 min	30	150.16 ± 127.93
Skrúður	-13.63	2014	2016/17	1 min	52	93.55 ± 85.52
St. Ulvøyhomen	14.85	2008	2008/09	10 sec	145	101.17
Storstappen	25.5	2008	2007–09	10 sec	196	145.16

*Total distance from 2011 only

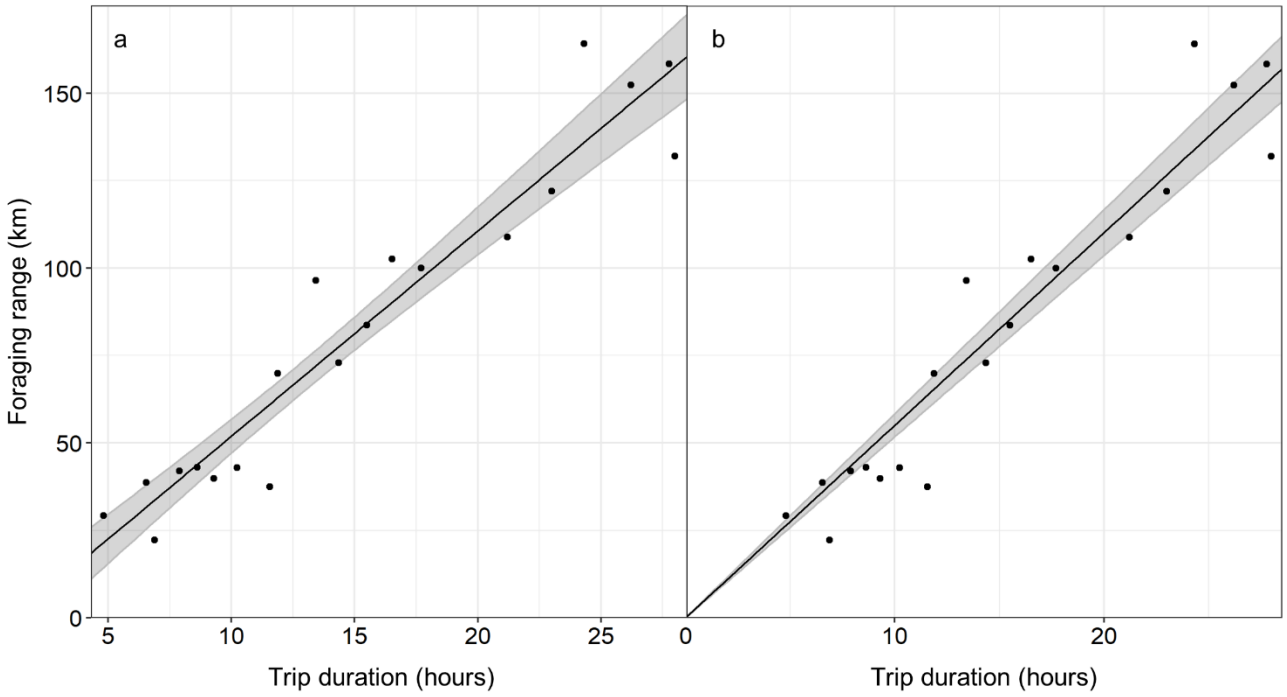


Figure S6.2. Mean trip duration and mean foraging range for 20 northern gannet *Morus bassanus* colonies. Predictions (black lines) ± 95% confidence intervals (grey ribbons) from a) a Linear Model and b) a Linear Model with the intercept fixed at zero (both fitted with the finite population correction). Duration was highly correlated with range, with a pseudo r^2 of 0.92 ($2logLR_{1,18}$ = 259.871, $p < 0.001$) or 0.98 with a zero intercept ($2logLR_{1,19}$ = 1087.275, $p < 0.001$). Regression equations were a) y = 5.87x - 6.78, b) or y = 5.51x with a zero intercept (y = range, x = duration). Our regression equations broadly agree with, but had a shallower slope, than y = 7.05x used in Lewis *et al.* (2001) and Davies *et al.* (2013). A variable intercept is more appropriate as foraging trips cannot be zero.

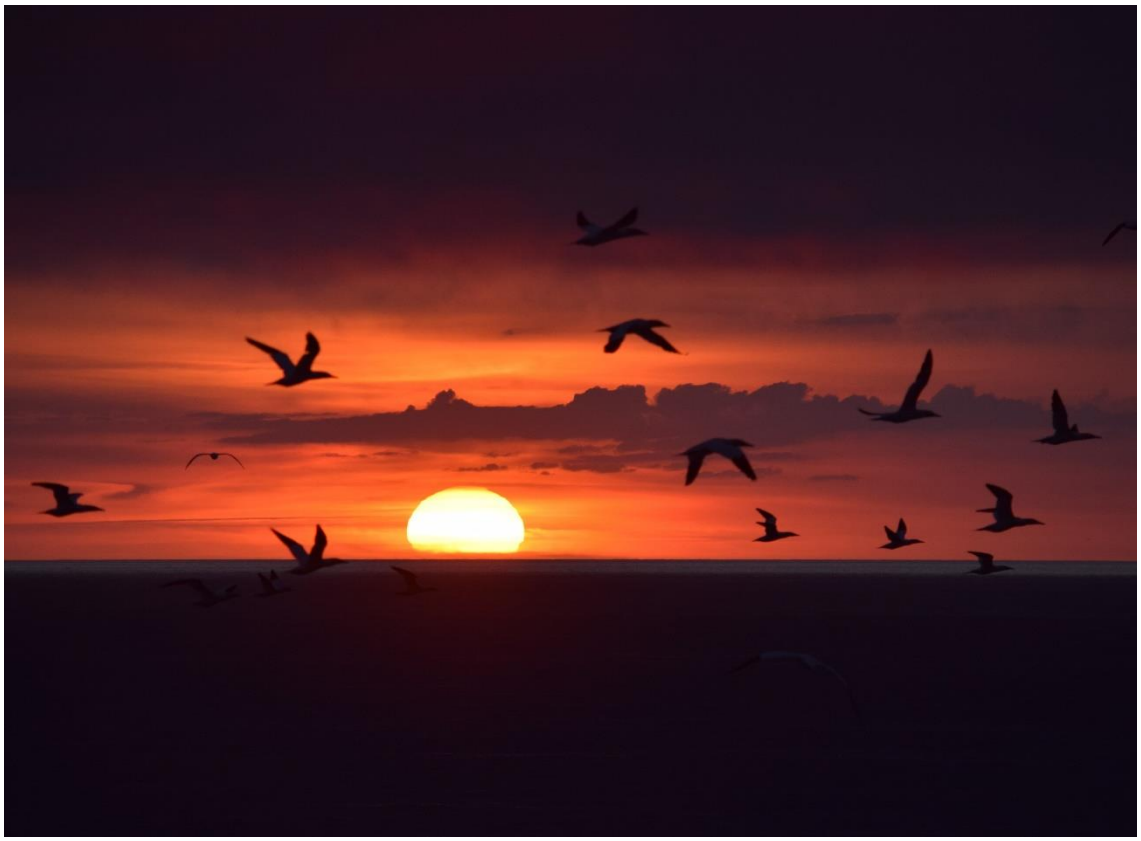
Table S6.2. Parameters estimates for Linear Models fitted with the finite population correction explaining northern gannet *Morus bassanus* colony means for foraging trip duration and range. Models contain the 14 colonies for which >10 individuals were tracked. Whole model pseudo r^2 is 0.78 for duration and 0.76 for range. Delta (Δ) pseudo r^2 is the difference in pseudo r^2 with and without the variable included. CI = Confidence Interval.

Variable	Explanatory variable	Estimate ± SE	95% CIs	2logLR	d. f.	p value	Δ pseudo r^2
Duration (h) ~	Intercept	28.949 ± 8.074	13.123, 44.775	-	-	-	-
	√Colony size	0.072 ± 0.010	0.052, 0.091	52.432	1, 11	<0.001	0.41
	Latitude	-0.374 ± 0.124	-0.617, -0.130	9.038	1, 11	0.013	0.10
Range (km) ~	Intercept	139.37 ± 45.03	51.11, 227.63	-	-	-	-
	√Colony size	0.441 ± 0.067	0.309, 0.573	42.842	1, 11	<0.001	0.45
	Latitude	-1.789 ± 0.683	-3.128, -0.450	6.86	1, 11	0.025	0.06

Table S6.3. For colonies where more than one year of tracking data is available, annual means for foraging trip duration, range and total distance ± standard error or *standard deviation where available. Colony size is given in Apparently Occupied Sites or Apparently Occupied Nests.

Colony	GPS year	GPS data source	n birds	n trips	Duration (hours)	Range (km)	Total dist. (km)	GPS freq.	Count year	Colony size
Alderney	2011	Warwick-Evans *et al.* 2016a	17	37	16.6±2.1	106±9.9	331±34	2m	2011	7,885
	2013		15	72	23.5±3.3	121.4±16.7	390.3±54.4			
	2014		13	83	20.9±3.3	114.5±16.4	378.3±53.1			
	2015		15	96	27.0±2.4	135±7	476±22			
Funk Island	2003	Garthe *et al.* 2011	7	11	14.9±5.0*	62±12*	177±49*	3m	2004	10,047
	2005		19	23	17.3±9.6*	122±81*	353±222*			
Grassholm	2006	Chapter 2	23	29	24.8±3.4	123.7±16.8	375.1±276.9	3m	2004	32,094
	2010		86	22	24.1±1.6	150.5±10.7	466.1±33.6	1 or 2m	2009	39,292
	2011		203	45	20.8±1.4	109.1±4.9	358.1±19.4			
	2012		47	40	23.8±1.8	130±8.8	428.4±31.3			
	2013		47	76	20.7±1.4	126.0±7.0	412.0±26.8	1 or 2m	2015	36,011
	2014		41	50	17.9±1.4	122.8±8.5	367.2±25.8			
	2015		27	41	18.4±1.4	94.7±5.7	332.5±21.9			
	2016		38	67	17.1±1.8	72.7±5.7	231.1±22.8			
	2017		21	35	38.0±3.8	137.7±8.6	519.0±59.6			
Great Saltee	1999	Hamer *et al.* 2001	5	54	11.9±6.7*	89±49*	NA	180m	2004	2,446
	2011	Wakefield *et al.* 2013	18	162	16.7±11.5*	81.9±52.3*	265.8±177.6*	2m	2004	2,446
Bempton	2010	Langston *et al.* 2013	12	1272	8.6	43.2	126.5	~1m	2012	11,061
	2011		4	574	8.2	37.2	119.6			
	2012		9	945	8.9	46.2	133.3			
Bass Rock	1998	Hamer *et al.* 2007	14	70	31.5±13.0*	224.3±96.8*	588.2±245.5*	30m	2004	48,065
	2002		13	42	40.0±17.6*	319.7±132.9*	786.0±344.3*			
	2003		21	58	25.9±9.6*	170.5±94.2*	417.6±231.3*			
	2011	Wakefield *et al.* 2013	28	124	27.8±15.8*	158.4±69.1*	503.4±250.4*	2m	2009	60,953
Vestmann-aeyjar	2016	Clark *et al.* 2019	2	23	10.8±1.3	51.0±4.8	153.1±18.0	2m	2013/2014	15,044
	2017		7	13	9.3±2.6	28.7±7.9	116.3±32.7	1m		
Skrúður	2016		13	30	5.8±1.0	33.8±5.1	93.8±13.9	1m	2014	6,051
	2017		15	41	4.1±0.6	25.9±3.3	75.1±66.8			
Store Ulvøyhomen	2008	Pettex *et al.* 2012	23	NA	7.4±0.9	25.3±3.4	114.8±13.6	10s	2008	308
	2009		20	NA	6.3±0.4	18.8±1.1	85.5±4.4			
Storstappen	2007		21	NA	4.5±0.6	19.8±2.2	89.1±9.4	10s	2008	1,244
	2008		23	NA	8.4±1.2	53.8±5.9	190.6±27.9			
	2009		14	NA	6.6±0.4	42.3±2.5	154.6±9.0			

Chapter 7 – General discussion



7.1 Summary

In this thesis, I investigated a range of factors that affect northern gannet *Morus bassanus* (hereafter "gannet") foraging behaviour: sex-specific niches, energetic costs, scavenging from fishing vessels, and the effect of latitude. This thesis made use of novel combinations of existing methods and comparison with existing data. The combined use of accelerometers with video cameras or altitude loggers revealed new information about the energetics of flight and seabird-fisheries interactions (Chapters 3 and 4). Repeating existing studies to create a long time series provided new inferences on the stability of niche partitioning and foraging effort (Chapters 2 and 6). Undertaking comparable studies in new regions provided valuable insights into ecology and behaviour under differing conditions in terms of climate and fisheries policy (Chapters 5 and 6). All chapters show the benefits of using multi-year and/or multi-region data to avoid spurious results based on specific samples.

In brief, the results from each chapter are as follows. In Chapter 2, I found that sex-specific niches varied over an 11-year period in foraging trip range, duration and timing; spatial distribution; and habitat selection, but remained consistent in isotopic niche segregation. This highlighted problems with drawing general inferences based on data collected in a single year at a single site. Chapter 3 used video-validated accelerometry to produce accurate activity budgets and revealed the relative energetic costs of different behaviours. This showed that behavioural time budgets and relative energetic costs were independent of trip duration, validating the use of GPS-derived metrics as a measure of foraging effort. In Chapter 4, bird-borne video cameras showed that 55% of recorded dives occurred at fishing vessels in Grassholm, UK, but that there were no differences in foraging effort between scavenging trips and natural foraging trips. Specialist scavengers may be vulnerable to reduced discards availability caused by changes in fisheries practice or policy, although this may be buffered by taking fish directly from trawl nets below the surface. Chapter 5 showed that gannets did not respond to fishing vessels in Iceland, where discarding is banned, and short trip durations may indicate plentiful natural food. Chapter 6 compared foraging effort for 20 gannet colonies across a large latitudinal scale to show that, when controlling for the strong effect of colony size, foraging effort decreases as latitude increases. This has the potential to facilitate northward shift in the range of the gannet, and other colonial species.

7.2 Further research

Our results suggest a number of lines of future enquiry. Here, I will outline these for each data chapter:

7.2.1 Chapter 2 – Sex-specific foraging

Chapter 2 showed that sex-specific foraging in gannets is more complex than previously known (see Stauss *et al.,* 2012; Cleasby *et al.,* 2015b), with a mixture of stable and variable aspects of niche segregation. As gannets are repeatable in foraging location within and, to some extent, between years (Patrick *et al.,* 2014; Votier *et al.,* 2017), it would be interesting to track the same males and females again in multiple years to investigate how interannual repeatability differs between males and females. This would help to address whether sex differences are driven by differing responses of males and females to prey availability.

Our results show that repeating studies across multiple years can provide new insights and as such, any studies of sex-specific foraging behaviour could be repeated in the same location to work towards a more general understanding of which aspects are stable or variable and what causes such variation. To further investigate the role of dimorphism, it would be valuable to study sex-specific foraging across 3-10 years in a range of species with different levels of size dimorphism. As such, a fruitful avenue of research would be to identify other studies that assess niche differentiation and repeat these under new environmental conditions to test its responsiveness to change. This approach would benefit studies of seabird sex-specific foraging, and could equally be applied to other taxa and other types of niche segregation, such as between species, age classes and morphs.

7.2.2 Chapter 3 – Foraging energetics

Validating accelerometry using animal-borne video footage has only recently been made possible due to improvements in biologging technology (Nakamura *et al.,* 2015; Watanabe & Takahashi, 2013). Previously, training datasets had to be created from visual observations of the tagged animals (e.g. Fehlmann *et al.,* 2017), which is not possible for many species that cannot be directly observed, including most birds and marine animals. We used bird-borne video cameras to create a training dataset, to produce a model for classifying behaviours gannet from acceleration data alone.

To quantify the relative energetic costs and time allocations of different behaviours, we first created a random forest model to classify behaviours based on accelerometry. The model used to classify behaviours in Chapter 3 had a low overall error rate, but the behaviours of some individuals were very well-described, while others had higher error rates (Chapter 3). This may relate to individual difference in tag placement (Vandenabeele *et al.,* 2011), behaviour or morphology (Suryan *et al.,* 2008; Vincze *et al.,* 2019), but also to weather conditions (Amélineau *et al.,* 2014). To improve the model, more examples of the behaviours that are most important, most likely to be mistaken, and better account for the variation should be added to the training dataset.

To develop this research, it would be valuable to produce a model for the behaviours of all gannets. To achieve this, we would first test the model using birds from other colonies that may have morphological differences, or experience different conditions. For example, in Iceland northern gannets are 10% heavier, with impacts on wing loading (Suryan et al., 2008), and they also moult primaries during the breeding season (pers. obs.), which may impact energetic costs of flight. A model that can correctly classify the behaviours of any gannet would allow for a multi-colony comparison of fine-scale activity budgets and the relative energetic costs of each behaviour. As such, it would be informative to compare these components of foraging effort for individuals of different colonies that are expected to vary in foraging behaviour due to differences in factors such as colony size (Davies *et al.,* 2013; Lewis *et al.,* 2001), environmental conditions (e.g. Montevecchi *et al.,* 2013; Pettex *et al.,* 2012; 2015; Warwick-Evans *et al.,* 2016a), and fisheries regimes (e.g. Bodey *et al.,* 2014; Camphuysen, Heessen & Winter, 1995).

We found a great deal of variation in the ODBA measured in relation to height gain. Possible explanations for this variation may be the energetic savings provided by flying in ‘V’ formations (Portugal *et al.,* 2014). As some video footage contained images of gannets flying closely behind others, this could be investigated. However, this was a rare occurrence as gannets are more likely to return to the colony in groups rather than leave the colony, and the battery life of the videos cameras was not sufficient to record the inbound part of the foraging trip (pers. obs.). Using video cameras with a delayed start or longer battery life could allow for the energetics of group flight to be assessed.

7.2.3 Chapter 4 – Scavenging behaviour

A key next step in understanding seabird-fisheries interactions will be to continue monitoring gannets on Grassholm using the same protocols to assess any changes in their attendance of fishing vessels after the full implementation of the discard ban (Commission of European Communities, 2009). This is particularly urgent in the context of the exit of the UK from the European Union as this may result in further changes to fisheries practice and policy within the British part of the Celtic Sea. Furthermore, it would be valuable to track the same individuals to quantify repeatability and potentially reliance on fisheries both within and between years. In particular, conducting a study in a year of poor natural prey availability could show how the importance of fisheries may vary. Furthermore, the availability of natural prey is likely to be impacted by climate change (Dias *et al.,* 2019; Grémillet & Boulinier, 2009). As the majority of gannets breed in the southern half of their range (Murray *et al.,* 2015a), the northward shift of their prey (Berge *et al.,* 2015; Dalpadado *et al.,* 2012; Astthorsson *et al.,* 2015) may cause gannets in areas of high levels of competition for natural food to rely more heavily on subsidies from fisheries. It is also important to compare the behaviours of plunge-diving gannets with surface feeding scavengers that may not be able to exploit vessels in the absence of discarding as proficiently as gannets can.

More broadly, bird-borne cameras can confirm that vessels are discarding, and that birds are stealing catch from nets under the water and engaging in interspecific interactions. As such, other systems could benefit from the use of animal-borne video cameras. For example, scavenging animals could be used to investigate the compliance of fisheries to discarding laws or general fishing laws. Illegal, unreported and unregulated (IUU) fishing is a major threat to fish stocks and the marine environment in general. While the use of remote sensing has greatly improved the monitoring of fisheries (Witt & Godley, 2007), validation of inferences from such data is key. Seabirds are ideal candidates as they often follow similar movement patterns to fishing vessels and target similar areas (Bertrand *et al.,* 2012; Xavier *et al.,* 2004). Bird-borne radar detectors have recorded undeclared radar signals that are likely to be associated with IUU activities (Weimerskirch *et al.,* 2018). Using bird-borne video cameras in combination with GPS loggers could show, for example, vessels fishing in no-take zones.

7.2.4 Chapter 5 – Responses to vessels in Iceland

In Iceland, we found that chick-rearing gannets did not respond to fishing vessels, provide a stark contrast with those in the Celtic Sea, where scavenging was common. It would be informative to conduct boat-based surveys in Icelandic waters to help understand the impacts on mixed-species flocks and include non-breeding gannets (it could be that only immatures or non-breeders use vessels, or that breeding birds use the vessels only during the non-breeding season). Filling in these gaps in the age classes and throughout the annual cycle would provide valuable insights into the importance and stability of this behaviour. The results of this chapter emphasise the benefits of repeating studies to provide comparisons with other regions. As such, it would be informative to conduct similar matched studies for other species.

7.2.5 Chapter 6 – Foraging effort and latitude

Collating comparable data from 20 gannet colonies allowed us to investigate a broad-scale spatial gradient in foraging effort. To further understand what drives variation in foraging effort, it would be informative to increase the number of tracked colonies. This would increase the number of hypothetically relevant variables able to be included in the model, such as temperature, temperature anomalies and the location and size of nearby gannet colonies. It would be particularly valuable to increase tracking in the north and south of the species range and over more years (as highlighted by Chapter 2), to cover a range of environmental conditions at each colony. Furthermore, it would be useful to have other metrics of effort, such as those derived from accelerometers for a sample of colonies (Chapter 3). Our results provide an important comparison to the Cape gannet (BirdLife International, 2018; Pichegru *et al.,* 2007) and the Australasian gannet (Angel *et al.,* 2015). Both species are limited by available land area at higher latitudes (Crawford *et al.,* 2015; Dunlop, 2009), so as the climate warms, they will not be able to respond by shifting their distribution poleward as the northern gannets have (Barrett *et al.,* 2017). A global assessment of the possible trajectories of seabird ranges in response to climate change and their physical limitations would be useful for prioritising mitigation efforts.

Range shifting in colonial species, including seabirds, is poorly understood. The formation of new colonies is particularly important due to the suitable range of species shifting with climate change. As we still do not have a

good understanding of how new colonies form (Grémillet & Boulinier, 2009), tracking of immatures and genetic studies may provide fruitful avenues to investigate this question. Additionally, repeated tracking at colonies as they change in size would allow us to disentangle the contribution of interannual variation produced by local conditions and that produced by population change (Davies *et al.,* 2013). To better understand these processes in general, it would be valuable to conduct similar studies for other species, and target tracking efforts to fill gaps in the data across the latitudinal range. Good candidates for this include the black-legged kittiwake *Rissa tridactyla* and the common guillemot *Uria aalge* as they have a similar distribution and have already been GPS-tracked in many locations (Parades *et al.,* 2012; Ponchon *et al.,* 2017; Wakefield *et al.,* 2017).

7.3 Conclusion

To conclude, this thesis provides new insights into a variety of aspects of gannet foraging behaviour: sex-specific niche segregation, energetics and the metrics used to measure effort, scavenging from fishing vessels and regional differences in responses to vessels, and a latitudinal gradient in foraging effort. These results could only be achieved by combining data types, and by collaborating with others to collect and collate data over extended temporal and spatial scales. As such, we show that the study of ecology can benefit from combining pre-existing methods into new combinations or extending the measurements across wider temporal and spatial scales to reveal new patterns.

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